The Journal of HEREDITY

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Trisomics in Spinach

Intersteller Migration

Multiple Lipomatosis

A Drosophila Counter

Linkage of Brachypodism

Twentieth Century Robinson Crusoe

VOLUME 50 MARCH-APRIL, 1959 NUMBER 2

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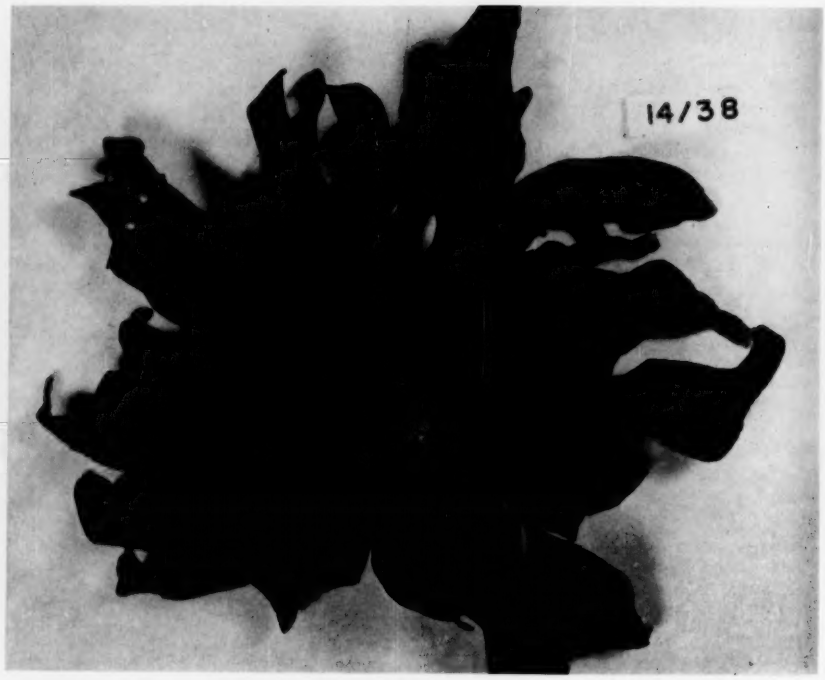

ABNORMAL TRISOMIC

Figure 1

An apparent abnormal *Star* trisomic in spinach.

THE TRISOMICS OF SPINACIA OLERACEA

JULES JANICK, D. L. MAHONEY, AND P. L. PFAHLER*

PRIMARY trisomics, or plants containing one extra chromosome in its entirety in addition to the normal somatic complement, have become extremly useful in genetics. They permit the rapid location of gene loci to particular chromosomes and in addition, enable the study of the phenotypic effects of individual chromosomes. Trisomics have been observed and studied in a number of species including *Oenothera lamarckiana*[4], *Matthiola incana*[3], *Datura stramonium*[1], *Lycopersicum esculentum*[7], *Zea mays*[8], *Triticum vulgare*[11], and *Antirrhinum majus*[10].

The present investigation of the trisomics in spinach ($n = 6$) is a part of a continuing study of the genetics of sex determination. One of the principal objectives has been to locate the chromosome pair containing the factor for sex determination. Dioecism in this species has been shown to be controlled by a mechanism that acts as a single factor pair, termed X and Y[5].

Methods

The material for this study was derived from a cross of diploid Nobel (N35) with a colchicine-induced tetraploid of Long Standing Bloomsdale (B119) made in 1953[6]. The resulting triploids were obtained from subsequent back-crosses to diploid Long Standing Bloomsdale. All plants were grown in the greenhouse. Chromosome counts were made from root tips fixed in Craf, sectioned in paraffin at 12 μ, stained with crystal violet, and counterstained with picric acid.

Production of Trisomics

Trisomics were first observed from cytological analyses of $2n$ ♀ × $3n$ ♂ crosses. Subsequently, trisomics were produced from the reciprocal cross. The distribution of progeny from these diploid-triploid crosses is presented in Table I. A greater transmission of seven to 12 chromosome gametes was found through the pistillate triploid than through the staminate triploid. There were over twice as many 13 chromosome plants produced when the pistillate rather than the staminate parent was triploid. The genetic and cytological implications of these crosses are presented elsewhere[9].

Description of Trisomics

From visual observations, variation among plants having 13 chromosomes arising from diploid-triploid crosses greatly exceeded variation within diploid or triploid plants derived from these same crosses. The trisomic plants growing vegetatively under short daylength were divided into six groups on the basis of their morphological appearance. Photographs of plants representing each of the six morphological types are presented in Figure 2. The names and de-

TABLE I. Distribution of progeny from crosses involving diploids and triploids in spinach

Cross	Chromosome number								Total plants
	12	13	14	15	16	17	18	19	
	(Percent)								
$2n$ ♀ × $3n$ ♂	49.3	17.9	0.5	---	1.2	11.4	18.9	0.8*	604
$3n$ ♀ × $2n$ ♂	27.5	36.1	7.0	0.9	2.8	12.5	13.1	---	327

*Obtained from one cross

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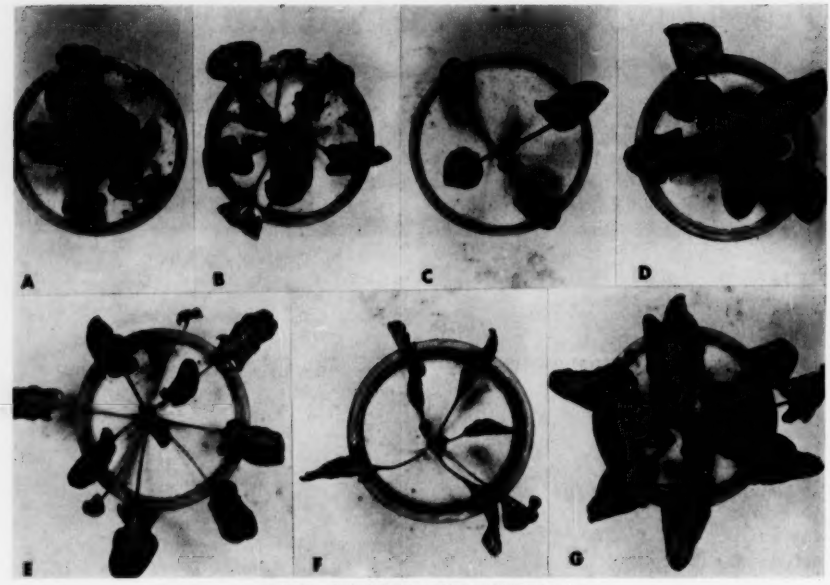

THE TRISOMICS OF SPINACH

Figure 2

A—savoy; B—oxtongue; C—reflex; D—wild; E—star; F—curled; G—diploid plant of Long Standing Bloomsdale, (pots are 5" in diameter).

scriptions are as follows:

savoy: Leaves extremely rugose, folded along midrib and curved when young; plant compact.

oxtongue: Leaves obtuse at tip, slightly rugose; plant spreading.

reflex: Leaves smooth, margins, recurved; plant greatly reduced in size and vigor.

wild: Plant phenotypically similar to diploid.

star: Leaves smooth, margins recurved, petioles long; plant spreading.

curled: Leaves extremely twisted, thick and rigid; plant reduced in vigor.

Two trisomic plants having an abnormal proliferation of leaves were observed in the *2n* ♀ × *3n* ♂ cross, one of which is shown in Figure 9. These were the only such plants observed in all of the trisomic types from diploid-triploid crosses. Examination indicated that these plants could possibly be classified into the *star* category. The mechanism responsible for this condition is not known. It may or may not have a direct relationship to the *star* trisomic.

The frequency and occurrence of the six morphological trisomics occurring in diploid-triploid crosses is shown in Table II. The frequency of five of the six

TABLE II. Distribution of morphological types of trisomic progeny from diploid-triploid crosses

Cross	Morphological type of trisomic progeny						Total classified trisomics
	Savoy	*Oxtongue*	*Star*	*Curled*	*Reflex*	*Wild*	
	(Percent)						
3n ♀ × *2n* ♂	16.5	23.8	16.5	13.8	8.3	21.1	109
2n ♀ × *3n* ♂	38.1	14.3	21.4	2.4	0.0	23.8	42

morphological trisomics obtained from the $3n$ ♀ × $2n$ ♂ crosses was similar. The *reflex* trisomic occurred the least frequently. In the $2n$ ♀ × $3n$ ♂ crosses the *reflex* trisomic was not observed and only one plant of the *curled* trisomic was produced. The frequency and occurrence of the six morphological trisomic types evidently depends on which of the parents is triploid. The differential frequency of the various trisomics from the $2n$ ♀ × $3n$ ♂ crosses may be a result of differential chromosome transmission to the male gametes or more probably to differential competitive effectiveness of the six types of $n + 1$ chromosome pollen.

Transmission of the Extra Chromosome Through Trisomics

Table III presents preliminary data from trisomic ♀ × diploid ♂ crosses, involving four of the morphological trisomics, *savoy, star, curled,* and *wild.* While the extra chromosome was transmitted in each cross, the frequency of transmission was less than the expected value of 50 percent. The data suggest variability within and between trisomics. Results from reciprocal crosses indicate that the extra chromosome is not transmitted through staminate trisomics. All progeny from diploid ♀ × trisomic ♂ crosses, presented in Table IV, appeared phenotypically diploid regardless of the morphology of the trisomic staminate parent.

Association of the Gene for Sex Determination with Its Morphological Trisomic

The genetic identification of the chromosome containing the gene for sex determination can be obtained by associating the factor for sex determination with a morphological trisomic, and then associating the trisomic with its corresponding chromosome. Genetic data from $2n$ ♀ × $3n$ ♂ crosses have shown that when the staminate triploid was simplex for the *Y* gene (*XXY*) the diploid progeny segregated 57 ♂ to 120 ♀, a ration of 1 ♂ : 2 ♀ as would be expected. In order to obtain staminate trisomics in the simplex condition for *Y*, trisomics were obtained from triploid or trisomic pistillate × diploid staminate crosses. Thus the staminate plant trisomic for the chromosome containing the sex factor would be genetically *XXY* and when crossed with the diploid pistillate would be expected to give diploid progeny in a ratio of 1 ♂ : 2 ♀. The other trisomics would be genetically *XY* and when crossed with the diploid pistillate would be expected to give progeny in a ratio of 1 ♂ : 1 ♀.

The results of the crosses of pistillate plants of Long Standing Bloomsdale with staminate plants of each trisomic, are shown in Table IV. One of the six morphological trisomics, *reflex,* produced progeny in a sex ratio not significantly different from 1 ♂ : 2 ♀ and therefore must be assumed to be that of the genotype *XXY.* The five other morphological trisomics gave ratios not significantly different from 1 ♂ : 1 ♀ and are assumed to be of the genotype *XY* and trisomic for one of the other five chromosomes. One *curled* trisomic crossed with three diploid pistillate plants gave nonhomogeneous populations of 10 ♂ : 58 ♀, 25 ♂ : 27 ♀, and 7 ♂ : 9 ♀. The ratio of 10 ♂ : 58 ♀ significantly deviated from either the 1 : 1 or 1 : 2 ratios. It might have arisen from contamination by selfing. Pistillate plants of Long Standing Bloomsdale produce an occasional staminate flower. This ratio was not included in the results presented in Table IV. The other ratios were homogeneous and were combined.

Discussion

The variation in 13 chromosome plants is composed of the effects of the addition of each one of the six chromosomes, and the effect due

TABLE III. Transmission of the extra chromosome in trisomic pistillate × diploid staminate crosses

Phenotype of trisomic pistillate parent	No. of plants in progeny	Percent transmission
savoy	269	34.5
	70	11.4
	58	8.6
	51	3.9
	41	7.3
star	30	30.0
curled	52	7.7
wild	10	20.0

TABLE IV. Segregation for sex in diploid pistillate × trisomic staminate crosses

Phenotype of staminate trisomic	Number of trisomics crossed	Total number of crosses	Progeny segregation		Chi Square for ratio	
			Staminate	Pistillate	1 ♂ : 1 ♀	1 ♂ : 2 ♀
Savoy	6	7	387	384	0	98.6**
Oxtongue	1	4	169	173	0	39.8**
Star	2	8	191	217	1.7	33.36**
Curled	2	6	218	226	0.1	49.7**
Reflex	1	3	74	143	21.9**	0.1
Wild	6	27	1116	1148	0.5	259.6**

**Significantly different at one percent probability level

to heterozygosity of the material. While cytological proof is not presently available the variation between types and relative uniformity within types indicates that the six morphological groups correspond to the six primary trisomics. The preliminary transmission data from four of the trisomics and the genetic data support this classification.

The differential morphological effects of each of the six chromosomes is quite remarkable, varying from no perceptible phenotypic change in the *wild* trisomic to the extreme modifications found in the *curled* and *reflex* trisomics. These morphological descriptions are from plants of a genetic background based largely on the variety Long Standing Bloomsdale. The morphology of these trisomics undoubtedly will depend upon the genetic background involved. It would be of interest to distinguish the effects of individual genes, as well as whole genotypes represented by diverse inbred lines, on the morphology of each of the trisomics.

The absence of transmission of $n + 1$ gametes through the staminate trisomic is interesting because $n + 1$ gametes are transmitted through staminate triploids. Previous studies[6] have indicated that the distribution of the six "extra" chromosomes in anaphase I of meiosis is at random in staminate triploids. However progeny segregation of $2n$ ♀ × $3n$ ♂ crosses as presented in Table I shows that the $n + 1$ pollen which theoretically should represent 6/64 (9.4 percent) of the total gametes in triploids produce 17.9 percent of the progeny. Similarly the n pollen which should represent 1/64 (1.6 percent) of the total gametes, produce 49.3 percent of the progeny. This is a viability advantage of the n over the $n + 1$ pollen of 16.4 to 1. Using these calculations, 5.7 percent of the progeny from diploid ♀ × trisomic ♂ crosses might be expected to be trisomic. The lack of trisomics from these crosses indicated that seven chromosome pollen probably cannot compete with normal six chromosome pollen. The aneuploid types produced in $2n$ ♀ × $3n$ ♂ crosses may be produced in situations where six chromosome pollen is not present on the pistil. This could be checked by dilute pollinations.

The trisomics of spinach offer an opportunity to investigate more intensively the genetics and cytology of this dioecious species. By employing similar techniques to that used in associating the trisomic *reflex* with the factor for sex determination, all of the other five linkage groups may be distinguished. Additional cytological investigations are in progress to associate each morphological trisomic with its corresponding chromosome. The identification of the chromosome associated with the *reflex* trisomic would be particularly interesting in view of the recent reports by Zoschke[12] and Dressler[2] of heteromorphic sex chromosomes in two varieties of spinach, which conflict with earlier investigations in this species. Intensive cytological and genetic studies on the chromosome pair containing the factor for sex determination in spinach should yield insights into the development of heteromorphic chromosomes and also into the problem of sex determination in all plants.

Summary

Six trisomic types were produced from crosses of triploid pistillate × diploid staminate crosses in *Spinacia oleracea* L., ($n = 6$). These trisomics were named in accordance with some distinct morphological characteristic *viz, savoy, oxtongue, star, curled, reflex,* and *wild*. Diploid-trisomic crosses indicated that the extra chromosome was not transmitted through any of the staminate trisomics but was transmitted through the four pistillate trisomics investigated. The gene for sex determination was shown to be located on the chromosome associated with the *reflex* trisomic.

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HEREDITARY MULTIPLE LIPOMATOSIS

F. E. Stephens and Arnold Isaacson

LIPOMATA are subcutaneous fatty tumors occurring singly or in multiple form on the body. Isolated cases are frequently found in the general population, but hereditary multiple lipomata is relatively rare. One of the kindreds studied in the Laboratory of Human Genetics at the University of Utah (Kindred 184) is of special interest because of the high frequency of multiple lipomata which it contains.

Description of Trait

In Kindred 184 the lipomata vary from pea-size to egg-size. There are usually more than one on an affected individual; there may be over one hundred. Generally lipomata first appeared at around 35 years, although age of onset varied somewhat, one case being reported as early as nine years. They are normally painless, although one individual did report pain when the tumors first occurred. In some cases the tumors first appeared in areas where the body regularly came in contact with some object such as a desk. They continued to grow, unless removed, until they became as large as a hen's egg. In no case in the kindred did any of the lipomata become malignant.

Figure 3 shows an individual badly affected with lipomata.

LIPOMATOSIS

Figure 3

An individual badly afflicted with lipomata is shown above.

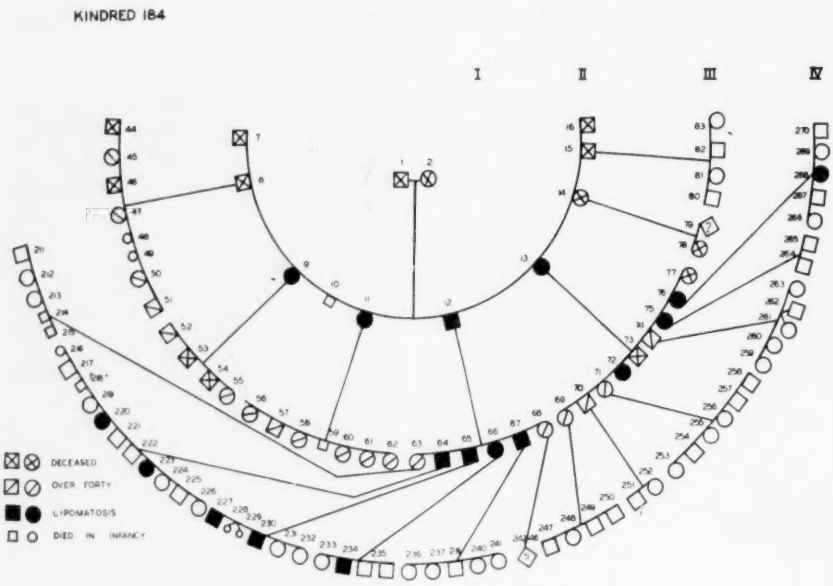
Literature

There has been occasional mention in the literature of familial cases of multiple lipomata. Leven[3] reported a family having seven affected cases in two generations, one female and six males. The age of onset was in the third decade of life.

Cockayne[2] published a pedigree from Hanhart of a Swiss family where lipomata were associated with tylosis of the feet and hands. Five males were affected in three generations. He cited several cases in the literature where multiple lipomata were familial in nature. He also gave data from workers which indicated a greater frequency of affected males than females in segregating sibships. He suggested dominant inheritance with possibly two genes being involved. He also thought that the condition might be partially sex-linked.

Hellier[4] reported a case where five out of 10 children had lipomata. The lipomata varied in size from the size of a pea to the size of a walnut.

*Laboratory of Human Genetics, University of Utah. This study was supported by a field investigation grant from the National Cancer Institute, of the National Institutes of Health, Public Health Service.



KINDRED 184

Figure 4

The pedigree of Kindred 184 is shown above.

Bonnefous and Valdequie[1] examined the blood of twin sisters having lipomata and found them to have a blood cholesterol of 396 and 414 mg. percent, respectively.

Knrzweg and Spencer[5] reviewed reports on 24 families having lipomatosis that had been reported in the literature before the publications of their work. They concluded that the numbers of affected individuals were too small to justify drawing definite conclusions on the inheritance of the trait. Their work included but three cases of affected individuals.

Shanks *et al.*[6] reported a study of multiple lipomatosis in two kindreds. One kindred showed one and the other kindred showed 15 affected cases. The authors concluded that multiple lipomatosis was inherited as a simple Mendelian dominant trait.

Kindred 184

Kindred 184 (Figure 4) consists of the descendants of I-2 who emigrated to this country from England. He had two wives. By the first wife he had four children, none of whom had any lipomata, nor did any of their descendants. He had 10 children by the second wife. Two of these, II-9 and II-11, were each reported to have had a lipoma on his forearm, but none of the descendants of these two seem to have been affected. Two other children, II-12 and II-13 both had multiple lipomata. Four of the six children of II-12 and six of his grandchildren were affected. Three of the nine children of II-13 and one of her grandchildren were affected. In all, 17 individuals in three different generations have had lipomata. Ten of the affected were females and seven were males. Figure 4 is a pedigree chart of Kindred 184.

Inheritance

The problem of identifying all the individuals in the kindred carrying the defective gene is difficult since (a) the trait is not normally expressed until about 35 years of age, (b) although the tumors were numerous in some, they were very few in others and could have been overlooked in those already dead, and (c) solitary lipomata are not infrequent in the general population. In addition, reports of relatives as to persons now dead may not be completely dependable, especially where, as in this case, the trait is not disabling and is considered to be of little importance by the family. For instance, II-9 and II-11 were both reported as having a lump on one of their arms; it is perfectly possible that these were not actually lipomata, or that they were merely chance cases. As mentioned above, none of their descendants, so far as known, have as yet developed the defect.

On the other hand, it is quite clear that II-12 and II-13 definitely had multiple lipomata and have transmitted the tendency to produce them to some of their children and some of their grandchildren. When we make allowances for many of the grandchildren being below the age when the tumors usually occur we have a very good picture of simple dominant inheritance.

Summary

The study of a kindred has been made which has 17 cases of lipomata in three generations. It occurs approximately equally often in males and females. If we make allowance for many of the grandchildren being below the age at which lipomata usually occurs, the data indicate simple dominant inheritance.

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CHLOROPHYLL MUTANT IN SOYBEANS PROVIDES TEACHING AID

Charles R. Weber and M. G. Weiss*

A GENE that conditions the development of chlorophyll in soybeans (*Glycine max* (L.) Merrill) has proved of value in providing a convenient genetics teaching aid. The genetic symbol assigned to the gene is y_{11}, and the $Y_{11}y_{11}$ type has been designated as T219 in the Soybean Genetic Type Collection maintained by the U. S. Regional Soybean Laboratory. Progenies from heterozygous plants segregate in a ratio of 1 normal green: 2 light green: 1 bright yellow (lethal). Segregating populations are effective in demonstrating a monogenic ratio as the three genetic classes are readily distinguishable in the seedling stage.

The y_{11} gene originated in a soybean plant (A691-1) of the F_8 generation from the cross Richland × Linman 533. Leaves on the main axis and branches at nodes three (first compound leaf node) through seven had yellow chimeric sectors. All leaves below the third and above the seventh node were normal green, and normal green plants resulted from seed borne at these nodes. Plants from seed produced at nodes bearing sectored leaves segregated as follows: 1 $Y_{11}Y_{11}$ (normal green): 2

*Agronomists, Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, and senior author additionally is Professor of Agronomy (Farm Crops), Iowa State University of Science and Technology. Joint contribution from the Iowa Agricultural Experiment Station, Ames, Iowa, and the Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture. Journal Paper No. J-3585 of the Iowa Agricultural and Home Economics Experiment Station, Project No. 1179, and No. 329 of the U. S. Regional Soybean Laboratory.

Y_{ny_n} (light green) : 1 y_{ny_n} (yellow, lethal). No sectored chimeric plants were observed in subsequent generations.

The monogenic theory was established on the basis of segregation in the first, second and third generations of seeds borne on the sectored portions of the original plant, and in the F_2 generation of four crosses with other genetic stocks as follows:

Homozygous yellow plants die when cotyledonary reserves are exhausted. The differential green of the homozygous dominant and heterozygous plants persists until shortly before maturity and facilitates selection of heterozygous plants for propagation. Although the vigor of heterozygous plants is somewhat below that of the normal green segregates, seed production is not seriously impaired.

Generation	*Seed Source*	*Number of plants*		
		Green	*Light green*	*Yellow lethal*
First	Sectored leaves and branches of original plant	20	26	16
Second	Heterozygous plants	91	171	76
Third	Heterozygous plants	56	123	55
F_2	Four crosses with other genetic stocks	561	1107	584
Observed		728	1427	731
Expected		721.5	1443	721.5

P = .9-.8

TWENTIETH CENTURY ROBINSON CRUSOE*

GLADYS C. SCHWESINGER†

PEOPLE who have been reared, or who have spent the greater part of their lives in socially and culturally isolated places, are of special interest to the student of nature-nurture influences. The first widely cited study of such a group was that published in England by Gordon[2] in 1923 on canal-boat and gypsy children. Gordon's 76 *canal-boat children* could attend school only 5 percent of ordinary school time, and only when their parents' canal boats were tied up for loading or unloading cargo. The average IQ of these children was found to be 69.6, at the borderline of mental deficiency. But what was equally striking was that the average IQ declined sharply with age, the 12 to 22 year-old group averaging only IQ 60, while the four to six year-olds averaged IQ 90! This suggested that IQ 60 might be a sort of upper limit for mental development under severely reduced school opportunity and the kind of home provided by canal-boat families. Gordon's findings on *gypsy children* were similar but somewhat less extreme as the gypsy children averaged 34.95 percent school attendance, had more social contacts outside of their families and were, therefore, less isolated.

Age Decrement

The coefficient of correlation between IQ and age for the canal-boat group was —.755; for the gypsy group—.439, suggesting that the differential effects of inadequate schooling and meager home culture become increasingly marked with age.

Age decrement has been reported for other underprivileged groups also; especially where educational facilities were deficient, such as for southern mill-town children of low socio-economic level in America[4]; children in orphanages coming from very inferior homes[13]; or from "high delinquency" areas in cities[8]; and for many investigations on rural children whose educational opportunities were extremely restricted and whose school attendance was aggravated by poor and impassable winter roads, the need of child help on the farms in spring and fall, short school terms, and so on. Studies of thousands of rural school populations in all parts of the United States have consistently revealed inferior scores for rural children, and all show the age decrement: little or no difference at the pre-school levels, progressively lower average IQ for each subsequent age level; until at ages 15 to 18, the retardation in IQ amounts to at least 10 points on the average.

Selective Migration in Rural-Urban Movements

Pressey and Thomas[9] found that the children of "poor" farming districts (i.e. those from poor, inferior soil and hilly land) scored lower than did the children from "good" farming districts. European studies, conducted by Klineberg[5], and Rosca[10] in Rumania, showed equally striking urban-rural differences. The greater deficiency in school facilities and the lower socio-economic level in the homes which always seemed to accompany the lower-scoring group suggested a constant, selective process.

Opposed to the rural drop, however, were findings in Great Britain[1,14] especially in the Scottish surveys[11] which report relatively no difference in mean IQ's between urban areas, industrial belts, entire rural areas, and the more isolated rural districts of the Scottish Highlands and Islands. The observation of Rusk, the director of the surveys, is pertinent: "perhaps nowhere else has scholastic opportunity been more evenly equated than in Scotland: 99.7 per cent of Scottish teachers are fully trained."[11] This means that children in the Highlands and Islands of Scotland may not really have suffered serious school deprivation at all! To account for the rural su-

**Crusoe of Lonesome Lake.* Leland Stowe. Random House New York. pp. 234. 1957. $3.50.

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periority, others have suggested that "selective migration" in reverse may have operated to draw the more intelligent persons from the cities, since in Britain rural living enjoys greater prestige than it does in many other countries!

Selective Migration in Urban-Rural Movements

Obviously, there are various reasons for migrations between city and country; and the caliber and quality of the migrants can vary with the reasons for the migration of the moment. In the beginning, the westward expansion of America drew off men of initiative and intelligence; of adventurous and courageous spirit. Land rushes, gold and oil discoveries, a quick response to the opening of far-flung railroads, which led progressive and energetic individuals to strike out into new territory, attracted the intelligent and the intrepid who were quick to see and to seize these new lures. As the pioneer centers settle down to normal living, in time, their children find life duller than their parents had; and seek their own personal opportunities in town. This could leave behind the less progressive and aggressive individuals; and such human drainage, operating over several generations, could eventually lead to a remaining residue of inferior stock. And as Klineberg found in the other direction[6,7], the intelligence test scores of the outgoing migrants to the cities would improve with their length of exposure to the newer opportunities of the city.

There is evidence also to suggest that migrants who are drawn to cities may represent both extremes of the population distribution[3,15]. On the one hand, the more alert, more ambitious, and more intelligent will respond to the superior opportunities of the cities; while on the other hand, the more hopeless and destitute who had eked out a bare existence on the soil, will also want to go to brighter fields. What people do with their new opportunities in the way of creative, personal development from then on will depend not only on the stimulation of the new homes, but also on that elusive something once referred to as the "quality of the organism." A second observation to be drawn at this point is that the selective migration factor will manifest itself in culturally deprived environments as well as in culturally rich ones. Original mental material, working in close cooperation with motivation and purpose, can profit not only from improved environmental facilities, but should respond equally to the challenges of a restricted environment in such a way as to differentiate the capable from the less capable.

Ralph Edwards, Crusoe Extraordinary

Five foot, five in stature, with only a fourth-grade education, and with previous experiences limited to that of a farm-hand, Ralph Edwards, at 21, in 1912, entered the impenetrable hinterland mountains and frozen lakes east of the Bella Coola Valley in British Columbia. In his pocket were four years of savings, while in his head was a little "know-how", acquired from books written for college students of agriculture which, like Abraham Lincoln, Ralph had studied by candlelight after the heavy, 12 hour work-day on his employer's farm was over. In uncharted territory, Ralph found and staked a homestead so far beyond human habitation that to this day, it has not yet been serviced with a passable road! A native trapper helped him to pack in his initial supplies on horseback as far as a horse could make it, and thenceforward, with 70 pounds apiece on their backs, the two men set out through heavy undergrowth, over rocks and boulders and rockslides, up steep cliffs, across streams and rivers, and over the most formidable terrain, making successive trips until 600 pounds of supplies and equipment had been transferred to the head of a breathlessly beautiful lake, there to be put on a large sled—self-made of course—and pulled seven miles up the frozen waters by shoulder-strapped ropes and human muscle power.

Edwards was then left alone to face his problems. With only a smattering of the woodsman's lore, he felled 100-foot fir trees, built a log cabin, cleared land, shot game, fished from the streams, tackled grizzly bears, moose, wolves, and other wild animals, and through a winter of 40° below and lower, endured such exceedingly great loneliness that only the severe demands of his work could dispel it. Came spring, and he planted vegetables before leaving to hire out for paid work in Bella Coola, some fifty miles on the other side of his back-breaking mountains. For several summers in a row, Edwards earned his cash this way, returning each fall to clear more land on his homestead and construct a permanent home for himself and the family he looked forward to having. An untrained and unskilled beginner, he made towing rafts for lake transportation, hewed out a big cedar log and shaped it into a canoe, built a trolley-line from the native woods for lifting and moving 12-foot logs across the 300 yards of clearing to his selected cabin site, and erected them into place to form his log house, all, all alone!

In 1917, Edwards took leave of his self-made furniture, his expanding acreage of cleared land, and his three-roomed house to join the American Expeditionary Force in the First World War. Two years later, he picked up where he had left off, applying his new army skill with rifle and knife, and carefully allocating his saved-up army pay to the purchase of a horse, a heifer, three steers, a variety of tools, and a stumppuller, all of which, by characteristic herculean efforts, he managed to get across the mountains to his homestead alone. On one trip out for store supplies, in 1922, he met an 18-year-old girl in Firvale, a tiny hamlet 20 miles away, itself only a spot in the wilderness. A year later, Ralph and Ethel Edwards worked side-by-side to improve their

home, the husband spending much of his time trapping and hunting, the wife staying home to do its never-ending work, and later to care for three children who came to bless their loneliness.

One day, a terrific misfortune overtook them when a flash fire razed their log house and everything in it, stranding the little family in the wilderness without food, clothing, shelter, equipment, money, or near neighbors to take them in. Again character and integrity paid off; for it was these alone which brought the Edwards credit and encouragement to try again. Once more, the pioneer family set about building a new house and producing quantities of home-grown food, home-made clothing, and equipment. They made their shoes from leather which they tanned according to instructions given in government pamphlets; they spun their wool and made their own socks; they fashioned their own snowshoes from local maple and cowhide and bearhide. Ralph stocked the uninhabited waters of a local lake with trout, and today it swarms with fish. He brought in farm equipment by taking his machines apart and discarding all the wooden parts that were too bulky to go along the impassable mountain trail (and these he later duplicated by the "do it yourself" method). Carrying in the metal parts required several trips, while the reconstruction of each piece of equipment was done from memory and local timber. In time, and by the same method, Ralph imported a small generator to make it possible for his home to have electricity. This brought out the need for a sawmill, which he also built by studying "Millwrights and Mechanics Guide," using split-half milk tins, a self-hewed water wheel, and an eight-strand, self-made rawhide 160-foot rope!

As their children grew into school age, the Edwards' had no choice but to use the correspondence-course method, which Ralph and his wife—herself only rurally-schooled—stimulated and supervised. The parents' self-education progressed with that of their children. Today, their library consists of several hundred well-selected volumes in cytology, paleontology, entomology, music, geographical and literary works of the first order. The Edwards children learned from the world of nature outside, their observation power sharpened under their parents' tutelage. In time, the youngest child, Trudy, was examined by a university professor and found to have a knowledge of botany and zoology equivalent to that of a college degree!

It was this same girl, Trudy, who cultivated the confidence and protected the welfare of the last remaining trumpeter swans, *cygnus buccinator*, which even then were threatened with extinction. And it was Trudy Edwards and her father who assisted the Canadian Wild Life Service to trap and secure five of these noble birds for air transportation to England to be presented to the then Princess Elizabeth. In time, too, Trudy built a 30-foot bridge, hewed out a road up the valley, felled giant forest trees, erected a cabin for herself, and cleared acreage around it.

A long-time dream of the Edwards family was to own an airplane for quicker contact with the outside world. With no money, there was only one way to get it: the never-failing "do it yourself" way, and Ralph and his daughter proceeded to educate themselves in the complex field of aeronautics, through years of evening studies in mathematics from algebra to calculus, passing through meteorology and engineering to aircraft designing and the techniques of flying. They worked through one thick technical volume after another, solving problems of flutter and vibration and lift, all on their own. Ralph acquired an 85-horsepower Continental engine and, bit by bit, forged ahead in figuring the kind of body his craft would need. After 10 years of such plodding, and after achieving enough knowledge to know how to build an airplane, he was confronted one day with the crushing information that the government regulations would never clear his home-made craft for flying!

Immediately, father and daughter began to look for a second-hand plane which they could afford to buy and learn to fly. Ralph was 62 by then, and Trudy 24; so she was selected to go to Vancouver first to take flying instructions and to find a plane to bring back to Lonesome Lake. In two weeks, Trudy had her pilot's license and a 65-horsepower Taylorcraft plane, and promptly headed for home. It had taken her five days to reach Vancouver by foot, horseback, and coastal ship; but it required only 2½ hours to come back by air!

The following March, her father reported in Vancouver for his physical examination for a pilot's license, only to overwhelm the skeptical officials and physicians there. The oldest man in Canada ever to qualify for a pilot's license, Ralph was solo-flying after 28 hours of instruction!

With less than 17 hours of solo-flying in his log book, Ralph began airlifting his farm's produce over the rugged mountains of his home terrain to sell to markets beyond. Then the Taylorcraft's old engine conked out, and his long years of self-taught aeronautics paid off again, for he himself set out to make the necessary structural alterations and get the old Continental engine—which he had long before purchased but continued to keep in good condition—installed in his plane. He flew to Vacouver to have his alteration approved by the Department of Transport who, while shuddering at his many improvisations, were forced to give him his certificate; because there was no flaw in his calculations and adjustments!

Innate Capacity and Motivation: Their Significance for Development and Achievement

This is about where we came in on our discussion: How could Ralph Edwards, with only four years of formal schooling, and his children with only correspondence courses, accomplish

all this? There is only one answer: good innate capacity, tremendous backbone, high motivation, never-faltering purpose, and character as rugged as the terrain they conquered. The Ralph Edwards family reached their high level of mental and educational development in an isolation which social scientists would all concur in designating as one of such extreme cultural limitations that severe mental and educational retardation was to be expected!

And now, to strike a more personal note: Thirty years ago, Schieffelin (now Mrs. Bosanquet) and Schwesinger published a book "Mental Tests and Heredity"[12] which gave suggestions for further research on the intelligence of children in culturally deprived environments: Specifically, on page 277, it suggested a need for:

> "Studies on children in pioneer settlements who have had few cultural advantages or educational opportunities, but who are the offspring of progressive parents, as vs. the canal-boat and gypsy stocks in Gordon's study. Ref. Schwesinger."

At the time, Schwesinger (herself a native of British Columbia), daughter of pioneers, and niece of a homesteader, who four years earlier had preceded Ralph Edwards into the wild terrain of the Bella Coola Valley, was well acquainted with the caliber of the people who had pioneered her Province. Knowing them personally as she did, she was convinced that well-conducted research would disclose results quite in contrast to those found for children of lesser-calibered parents. She had a strong feeling that the environmental limitations of most of the groups reported on in the literature in the scientific journals were as much a reflection of the people who lived within them as a cause of their retardation and retrogression. Their very presence there stemmed from reasons quite different from the ambitions, the thirst for independence and a home of their own making and shaping, the progressiveness, which were the very essence of the spirit of the pioneers. When Schwesinger wrote the above-cited paragraph in 1930, she had even then in mind studying the very children in the very mountains behind the Bella Coola Valley where Stowe's book is set, but a depression came on, finances were not forthcoming to make the investigation, and her proposed study was never made!

And now, thirty years later, appears Leland Stowe's book, telling in one startling, dramatic activity after another, of what man can do who is equipped with initiative, grit, good native intelligence, and purpose. It remains now for the scientist to pick up where the journalist has pointed the way. Scientists will never be satisfied to draw deductions from a single case, and it behooves research psychologists who are interested in the nature-nurture tangle to follow up Mr. Stowe's signals and to design a study that will measure with scientific instruments the educational and mental level of numbers of backwoods children of the Bella Coola Valley. All the variables should be taken into consideration, of course; all the controls observed. But the opportunity should be seized, and seized now!

As the years go by, frontiers will fade out, but today in 1959, they are still there. East of Firvale, B. C., the terrain of the Bella Coola is still cut off from outside cultural contact. Before the road east becomes passable for ordinary conveyances, some research foundation should see the wisdom of financing a study not unlike the one proposed by the writer thirty years ago.

What offers?

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IRRADIATION AS AN AID IN FRUIT VARIETY IMPROVEMENT

I. Mutations in the Peach

L. Fredric Hough and Gerald M. Weaver*

THE possibility of inducing hereditary changes in plant and animal materials was first suggested by Muller[6] and Stadler[12] in the late 1920's. Soon afterward Stadler[13] reported the first X-irradiation of fruit tree material. Following their leadership, Schmidt[9] in Germany, Granhall[4] and Ehrenberg[3] in Sweden, and Bishop[2] in Canada began irradiation of fruit species. The useful mutants obtained from these studies have been largely confined to fruit color variants, as noted by Bishop[2] and again by Granhall[4]. With a steadily mounting interest in the application of peaceful uses of atomic energy since the beginning of the present decade, various institutions were given the opportunity to utilize the Cobalt 60 gamma field, described by Sparrow and Singleton[11], and by Shapiro[10], located at the Brookhaven National Laboratory, Upton, Long Island, to explore the possibility of efficient production of desirable mutants.

In fruit breeding projects much time is involved in deriving particular genotypic and phenotypic combinations by conventional hybridization methods. With the hope of accelerating this procedure, the present project was initiated in 1953. The first objective was to study the effects of chronic gamma irradiation on growth, flowering, and fruiting of fruit plants, with particular reference to the blueberry and peach. This paper is limited to a discussion of the mutations observed in peaches.

Materials and Methods

During the spring of 1953, 181 one-year-old peach trees of the varieties Brackett, Elberta, Erly Red Fre, Fairhaven, and Late Elberta were planted in the Brookhaven gamma field. At the same time 10 trees of each variety were established at New Brunswick, New Jersey, as controls. The young trees were arranged in arcs on concentric circles about the Cobalt 60 source with each variety represented one or more times at a particular dossage. The dosage ranged from 260 roentgens per day at the arc nearest the source to 10 roentgens per day at the most distant location. Following eight months' chronic exposure, 50 of the trees were removed and established in New Brunswick. Replacements were set in the gamma field in 1954 to fill vacant areas left by the previous year's removal or lack of survival. Following this second season, 75 trees which had received 20 months' chronic gamma irradiation and 50 trees exposed for eight months were removed from the gamma field. Seventy-five trees including eight and 20-month exposures were transplanted in New Brunswick and 50 were transferred to a control field at Brookhaven. The 1954 dose rates were slightly lower than those for 1953, due to the difference in the capacity of the source, which is partially renewed each winter in the reactor. Dose rates for the same planting distances ranged from 300 to 11 roentgens per day. Of all the transplanted trees, 170 survived, and it is on these trees that the present fruiting data have been compiled.

Results

The New Brunswick plantings fruited heavily in the summer of 1956. The

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trees at Brookhaven began to bear in 1957, although frosts during pollination season limited the fruit set.

Mutations in 1956

Two seasonal mutants were noted on the variety Fairhaven, which is a mid-season, tender, yellow-fleshed peach of better than average quality. These mutants exhibited both advance and delay in ripening season and consisted of whole branches. The early mutant resulted from eight months' chronic exposure of 32 roentgens per day, having received a total dosage of about 7,800 roentgens. Fruit on the affected branch ripened nine days prior to the normal date of ripening. There were seven fruit on the mutated branch. In the following year, 1957, this branch bore two dozen fruit. All except those on one spur were one week early in ripening. This spur contained two fruit; one ripened at the normal time, the second was early ripening. It would appear that this branch is a mericlinial chimera (as defined by Jones[5]), consisting of mutated and normal tissue. The sports for early ripening are compared at the peak of their maturity with the normal fruit in Figure 5. At the time of the photographing, the normal fruit were green-yellow and not quite up to the size of the brilliant red, early-ripening fruit.

The delayed-ripening Fairhaven mutant was induced by eight months' chronic exposure of 55 roentgens per day. Thus, the tree received a dosage of 13,500 roentgens. A number of changes were apparent. In 1956 the mutant branch bore some 50 fruit, all of which showed the mutated characteristics. The fruit ripened 21 days later than normal. The flesh was much firmer than that of Fairhaven. The vascular strands in the flesh were more conspicuous and the flesh was drier, almost mealy. There was an increased spread of anthocyanin throughout the flesh beyond the pit cavity (Figure 6), whereas only a slight amount surrounds the pit of the normal fruit. In addition to these features there was an increase in fruit size, presumably associated with the longer ripening season. In 1957 when the season was considerably drier and earlier, the mutant fruit ripened two weeks after Fairhaven. The anthocyanin pigment was less intense but the other characters persisted. There was also heightened color in the epidermis of the fruit.

FAIRHAVEN MUTANT

Figure 5

Nine days earlier ripening Fairhaven mutant above, normal below.

Additional mutations in 1957

Two additional early ripening mutants were observed on Fairhaven. These trees received 60 and 26 roentgens per day with total dosages of 36,300 and 17,000 roentgens respectively after 20 months' exposure. Both mutants bore fruit ripening one week earlier than normal.

In the variety Elberta, two mutants, each ripening two weeks later, were observed. The accumulated dosages were 2,450 roentgens (10 roentgens per day for eight months) and 15,700 roentgens (26 roentgens per day for 20 months).

ANTHOCYANIN COLORATION

Figure 6

Intense anthocyanin in flesh of late Fairhaven mutant below contrasted with the normal fruit above.

The latter of these mutants had appreciably firmer flesh and better quality.

A clingstone mutant was observed on a tree of the variety Brackett which had received an accumulated dose of 19,200 roentgens after 20 months' exposure to 33 roentgens per day. Five out of the six fruit on one branch were clingstone, indicating that this branch is a mericlinal chimera with regard to this character.

Discussion

The effects noted here demonstrate the possibility of producing genetic alterations in peaches through the use of ionizing radiation. These mutations have included changes in the season of ripening, in the flesh texture, in the freestone condition of the fruit, and in the pigmentation of the flesh and the skin.

The pattern of occurrence of the mutant character in the case of the early ripening mutant of Fairhaven first observed in 1956, and in the case of the clingstone mutant of Brackett, indicates that the shoots on which these mutants were observed are mericlinal chimeras. In view of the stratified nature of the dicotyledonous growing point (Schmidt[7]) probably all somatic mutations originate as mericlinal chimeras. With clonally propagated fruit plants all potentially valuable mutations should be propagated in such a way that the chimeral nature of each mutant can be determined. Obviously, each mutant must be isolated in the periclinal condition before it is propagated as an improved horticultural variety.

The nature of mericlinal chimeras is well illustrated by the distribution of flower colors on some branches of carnations reported by Sagawa and Mehlquist[7]. These mericlinal chimeral branches, or "partials" as designated by Sagawa and Mehlquist, were produced by X-radiation of varieties of carnations known to be periclinal chimeras. The mericlinal chimeras were not the result of somatic mutations, however, but were the result of radiation injury to the outer layers of cells in the growing point followed by restitution of this layer from genetically different cells. In addition to the changes resulting from destruction of cells in the growing points a few changes were observed which presumably resulted from somatic mutations.

In the present study of irradiated peaches, three mutations from the dominant to the recessive condition have been observed so far. These mutations involved genes governing the firmness and the freestone condition of the flesh. Bailey and French[1] have established that firm melting flesh is a recessive to soft melting flesh and that clingstone is recessive to freestone. The simplest mechanism to account for these three changes would be a change from the heterozygous dominant to the recessive condition through mutation or deletion of the dominant gene. The authors have had no opportunity to determine the genotype of Brackett with reference to the freestone-clingstone condition. However, the two mutations to firm flesh occurred in varieties known to be heterozygous for firm flesh. Elberta has moderately firm flesh but must be heterozygous for very firm flesh since seedlings with very firm flesh have been observed in progenies from Elberta. Fairhaven is heterozygous since it is a seedling of the very firm-fleshed variety, J. H. Hale.

In considering the immediate value of these radiation-induced mutations, the high-quality, firm, late-ripening sport of Elberta bears the greatest promise. Further testing will be required to determine whether the horticulturally

desirable tree type and productivity characteristic of Elberta remain unchanged. If so, this mutant should prove to be a valuable new commercial variety.

To increase the efficiency of irradiation as a technique in fruit variety improvement, additional information is needed on the interrelationships of dose rate and total dose at various critical stages of plant development. Current research along these lines includes continued chronic gamma irradiation; semi-chronic gamma exposures at high dose rates for short intervals during a particular phase of plant growth; and acute irradiation of pollen, seeds, and buds using various sources of radiation. Plant material possessing a high level of desirable horticultural characters is being used, so that the mutations which are induced will occur in combination with other highly desirable horticultural characters and therefore be of maximum value in further variety improvement.

Summary

Peach trees of five varieties were treated with Cobalt 60 gamma rays for one- and two-year periods at the Brookhaven National Laboratory gamma field. Mutations of potential value in variety improvement were produced on trees having received from 10 to 60 roentgens per day of chronic radiation throughout the growing season. Mutations were found in the season of ripening, firmness and texture of the flesh, and the freestone condition of the pit. A late mutant of Elberta holds promise of becoming a commercial variety and will be increased and subjected to further testing.

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LINKAGE IN LIMA BEANS

R. W. Allard and W. M. Clement*

THE lima bean species *Phaseolus lunatus* L. ($n = 11$) is comprised of a large number of genetic variants differing in conspicuous morphological characteristics. The inheritance of these characteristics is largely unexplored. Only 11 monogenic differences and two cases of linkage are reported in the literature[1-7,10,11]. There are two principal reasons for this paucity of information: Genetic observations on lima beans have usually been incidental to studies for a different purpose, and thus have seldom found their way into the literature. Additionally, linkages in this species have not been the subject of a systematic search.

During the past several years the authors have been engaged in studies of quantitative inheritance in lima beans. In the process, families became available that were segregating simultaneously for two or more monogenically inherited characteristics. These materials, supplemented with hybrids made specifically for the study of linkages, have been useful in identifying more than 20 previously unreported monogenically inherited character differences, and also in revealing 10 additional cases of linkage. This paper summarizes present information on linkage relationships and constructs a linkage map for the lima bean species.

Methods and Materials

Lima beans are highly self-pollinated in the environment of the Central Valley of California. Hybridization between strains is difficult because the smallness and morphology of the flowers make them difficult to manipulate. Consequently, though selfed generations are readily derived from heterozygous plants, backcrossed seeds cannot practically be produced in numbers large enough to be useful in linkage investigations. For these reasons, all recombination values reported here are based on data obtained from F_2 or F_3 families.

Recombination values were estimated by the product moment method whenever it was applicable, because this method is easily applied in conjunction with tables such as those of Immer and Henderson[9]. In many cases, however, both coupling and repulsion crosses were studied, or both F_2 and F_3 data were available. In still other cases, interallelic interactions made the product moment method either inapplicable or difficult to apply. When such complex data were encountered the recombination values were estimated by the method of maximum likelihood, a general method applicable to any genetic data that provides information about linkage. Maximum likelihood estimates of recombination values were computed with the aid of tables prepared by Allard[5].

Whenever a recombination value was based on more than one set of data, a heterogeneity test was applied to determine whether the data were consistent in supporting the combined estimate. The method followed was proposed by Fisher[8].

The loci tested for linkage are listed and described in Table I.

Experimental Results

The 90 linkage estimates reported in this paper were made from many different types of F_2 and F_3 families. In most instances, data for estimating a single recombination value were available from several different types of families. Since space is too limited for detailing these complex data, only the recombination values and their standard errors are listed.†

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†The detailed data are available from the Department of Agronomy, University of California, Davis, California.

Table II summarizes data on the 14 loci whose linkage relationships have been investigated most fully (63 out of 91 possible combinations). The linkage relationships of nine other loci, tested in only a few combinations, are presented in the text.

Ten previously unreported cases of linkage were discovered among the 90 combinations of loci screened for independence in two-factor segregations.

Linkage between d and wl

The *Wl wl* heterozygote is distinguishable from both homozygotes. Hence, in crosses segregating at the *wl* locus, six classes can be identified in the F_2 generation. Seven different F_2 families, four from *D Wl/d wl* and three from *D wl/d Wl* double heterozygotes, were studied to determine the independence of *wl* and *d*. All seven families agreed well in supporting the combined estimate of 2.1 ± 0.02 percent crossing-over between the two loci (heterogeneity $\chi^2 = 4.51$ for six degrees of freedom, $P = 0.70 - 0.50$).

Linkage between d and r

Crossing-over between these two loci has been reported on two previous occasions (Allard [5,6]). The estimate of the recombination value is but slightly altered by our later data which therefore are not discussed here.

Linkage between wl and r

From a combination of F_2 and F_3 data, the recombination value between *wl* and *r* was estimated to be 38.0 ± 1.3 percent, slightly less than the distance between *d* and *r*. Thus, the order of these three loci clearly cannot be *d r wl*. However, the information available is inadequate to differentiate between the orders *r wl d* and *r d wl*, although the map distance suggests that the first order is more likely. A procedure recommended by Smith[12] was used to establish the order positively. Starting with the coupling phase triple heterozygote *R Wl D/r wl d*, several thousand F_2 seeds were planted at a heavy rate, and all *D*-plants were rogued as soon as identified. Among the remaining plants, 14 were genotypically *Wl wl dd*. At the end of the season, when the *r* locus could be scored, 11 plants were *R*— and three were *rr*. Hence, the order is almost certainly *r wl d*.

Linkage between d and l_{13}

These two loci are very closely linked, the estimated recombination value being less than

TABLE I. List of loci tested for independence. The dominant form of the character is given first in each description

Symbol	Name	Description and Authority
D d	bush	Indeterminate (vine) vs. determinate (bush) habit of growth; Allard[3]
Wl wl	willow leaf	Lanceolate vs. ovate leaflet; heterozygote is intermediate (ovate-lanceolate); Allard[3]
R r	dark red	Dark-red vs. red seed coat; Allard[2]
S s	mottled seed coat	Mottled vs. self-colored seed coat; Rhind[11], Allard[2]
L_1 l_1	luteus	Green vs. yellow leaf; Allard, unpublished
Ms_1 ms_1	male sterile	Fertile vs. male sterile; Allard[4]
C c	basic color factor	Red vs. white seed coat. C is necessary for the expression of all other seed coat color genes; Allard[1,2]
G g	green cotyledon	White vs. green cotyledon, Magruder and Wester[10]
V v	variegated leaflet	Variegated vs. non-variegated leaflet; Allard[3]
P p	Red-purple seed coat	Red-purple vs. red seed coat; Allard[2]
Sr sr	red background color	Buff vs. red background color (expressed only in mottled genotype); Allard[2]
L_2 l_2	luteus	Green vs. yellow plant; Allard, unpublished
L_4 l_4	luteus	Green vs. yellow plant; Allard and Clement, unpublished
L_5 l_5	luteus	Green vs. yellow growing point; Allard and Clement, unpublished
Pi pi	purple intensifier	Purple vs. red-purple seed coat; Allard and Clement, unpublished
Rb rb	lavender-buff seed coat	Lavender-buff vs. dark-red seed coat; Allard[6]
L_{16} l_{16}	luteus	Green vs. yellow plant (induced by thermal neutrons), Allard and Clement, unpublished
L_{18} l_{18}	dwarf-luteus	Green vs. dwarf-yellow; Allard and Clement, unpublished
Z z	zebra	Self-colored vs. zebra-striped seed coat, Allard, unpublished
Cm cm	maroon	Red vs. maroon seed coat; Allard[6]
A_1 a_1	albino	Green vs. albino plant; Allard, unpublished
Cr cr	crinkled leaf	Normal vs. crinkled leaf; Allard[3]

0.1 percent. No attempt was made to establish the order of *wl d* and l_{10}, because very large populations would be required.

Linkage between d and l_4

Recombination between these loci was estimated from two F_3 repulsion families and 81 F_3 progenies derived from one of the F_2 families. The three sets of data were homogeneous and gave a combined estimate of 11.2 ± 1.74 percent crossing-over.

Linkage between wl and l_4

Homogeneous data from two coupling F_3 families and 80 F_3 progenies derived from one of the F_2 families gave a combined estimate of 12.4 ± 0.78 percent crossing-over between these loci. This suggests that l_4 lies on the opposite side of *d* from *r*. Unfortunately, data are not available on the distance between *r* and l_4, which would settle the question forthwith. However, with Smith's technique it has been possible to establish the order with considerable certainty. A large F_2 population was planted from seed derived from the triple heterozygote *D wl* l_4/*d Wl* L_4. Three *dd Wl wl* L_4- plants occurred, all L_4 l_4. The order of these three genes is therefore almost certainly l_4 *wl d*, not the order suggested by the map distances.

Linkage between d and l_5

Crossing-over between these loci was estimated from two F_3 repulsion families and from a single F_2 coupling family that was classified, by means of F_3 progeny tests, into the genotypes *D-* L_5 L_5, *D-* L_5 l_5, *D-* l_5 l_5, *dd* L_5 L_5, *dd* L_5 l_5, and *dd* l_5 l_5. The three sets of data gave a combined estimate of 39.0 ± 3.03 percent recombination, but this value is suspect since the data were heterogeneous (heterogenety χ^2 = 7.99 for two degrees of freedom, P = 0.02 – 0.01). Recombination values for the individual sets of data were as follows: family 1, 29.0 ± 6.3; family 2, 47.0 ± 5.4; and family 3, 45.9 ± 4.25 percent crossing-over.

The question of linkage between *d and* l_5 was settled by studying recombination between *wl* and l_5. This procedure was followed because the six-class F_2 segregation in the *Wl* L_5/*wl* l_5 hybrid provided greater efficiency of estimation than did the four-class F_2 segregation from the

TABLE II. Summary of linkage values in lima beans. The results of testing 63 out of 91 possible combinations among 14 loci are presented. The upper value in each cell is the recombination value and the lower figure the standard error of the recombination value. Combinations involving less thoroughly tested loci are given in the text.

	Wl wl	*Rr*	*Ss*	*L_1 l_1*	*Ms ms*	*Cc*	*Gg*	*Vv*	*Pp*	*Sr sr*	*Rb rb*	*L_3 l_3*	*L_5 l_5*
Dd	2.1* 0.02	39.3* 1.30	52.4 2.00	48.1 2.30	53.1 1.73	51.4 1.20	49.8 1.40	50.0 3.1	47.5 2.52	55.3 5.03	53.7 2.42		53.7 3.65
Wl wl		38.0* 2.61	47.3 3.02	47.7 3.28	48.8 2.88	50.3 1.55	50.4 3.19		49.1 2.94	53.7 4.25			42.8 4.27
Rr			51.9 1.73	52.7 2.21	54.6 4.02	49.3 3.02	52.6 1.36	52.9 0.93	45.9* 1.31	56.0 4.68	47.9 4.79	48.5 6.21	50.6 6.38
Ss				26.9* 3.13	54.9 16.9	52.0 3.18	48.0 2.42	45.1 3.66	46.3 2.70	46.1 3.31		55.5 4.95	43.1 6.69
L_1 l_1					48.2 3.44	45.3 2.63	50.4 3.37	49.7 1.87		49.5 5.23			
Ms ms						14.7* 0.83	43.1 8.05				48.6 7.45		
Cc							52.0 1.21	49.4 1.55	53.0 3.30	48.8 5.25	43.9 4.84	41.1* 3.28	43.2 5.04
Gg								52.6 2.00	52.3 4.00	46.3 6.8		47.4 5.45	
Vv									50.8 2.70				
Pp										59.4 4.77	38.2 6.75		
Sr sr													
Rb rb													
L_2 l_2													
L_3 l_3													

*Deviates significantly from p = 0.5

D l_5/d L_5 cross. The recombination between *wl* and l_5 was 50.5 ± 0.70 percent. Since *wl* and *d* are only two units apart, it seems almost certain that *d* and l_5 also are not linked.

Linkage between r and p

The recombination between these loci, 45.9 ± 1.31 percent, was estimated from five coupling phase F_2 families. The families were consistent in supporting this recombination value (Heterogeneity $\chi^2 = 8.371$, P = 0.10-0.05). Since the deviation from 0.50 is 3.13 times as large as its standard error, the probability that these loci are independent is approximately 0.001. Confirmatory data would be desirable before considering this linkage as positively established because of the looseness of the linkage.

Linkage between s and l_1

Positive identification of the *Ss* heterozygote is not possible in all hybrids segregating at the *s* locus. However, unambiguous classifications into *SS*, *Ss*, and *ss* genotypes could be made in the particular F_2 coupling phase family studied to determine the independence of *s* and l_1. The recombination value estimated from the six-class segregation in this family was 26.9 ± 3.13 percent.

Linkage between c and ms_1

The crossover value was estimated from nine different coupling phase F_2 families. However, the data were not consistent in supporting the combined estimate of 14.7 ± 0.83 percent (Unadjusted $\chi^2 = 18.70$ for eight degrees of freedom, P = 0.02 — 0.01). Crossover values estimated from the nine single families were 0.00, 0.05, 0.06, 0.07, 0.08, 0.14, 0.18, 0.21, and 0.33. Thus, though there is little reason to doubt that these loci are linked, the precise recombination value is uncertain. Three facts may have contributed to the significant heterogeneity: First, there was a significant deficiency of ms_1 ms_1 plants in three of the families studied. Second, pollen dispersal seems to be poorer in some seasons than in others with the result that occasional male-sterile plants are completely sterile in poor seasons and cannot be classified for the *Cc* segregation, although in good seasons all male-sterile plants set at least one seed. Third, fairly tight linkage caused a very few individuals to fall in recombination classes in some of the smaller families, and the unadjusted χ^2 test for heterogeneity was therefore not strictly valid. All of these factors would tend to inflate the χ^2 for heterogeneity.

Linkage between c and l_{16}

The recombination between these two loci, 21.9 ± 4.27 percent, was estimated from a single F_2 coupling phase family.

Linkage between c and l_2

The recombination between *c* and l_2, 41.1 ± 3.28 percent, also was estimated from a single coupling phase F_2 family. Since the deviation from 0.50 is 2.71 times as large as its standard error, the probability that these two loci are independent lies between P = 0.01 and 0.001. However, this linkage cannot be considered definitely established without confirmatory data.

Linkage between b and g

Bemis[7] reported that the *b* and *g* loci are linked, with 30 ± 3.7 percent crossing-over, but that *b* is independent of *c*, *r*, and *p*.

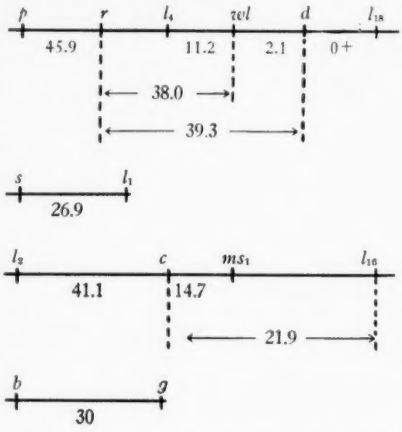
Additional Independent Loci

Data not included in Table II are available on 18 independent combinations, as follows:

d with: *cr*, 51.1 ± 5.43; *z*, 51.3 ± 3.83; a_1, 46.3 ± 5.04.
wl with: *pi*, 36.1 ± 9.03.
r with: *cm*, 46.1 ± 4.57; *z*, 56.5 ± 4.72; l_{18}, 53.1 ± 19.7 (both *r* and l_{18} are in linkage group 1); a_1, 54.0 ± 4.91.
s with: *z*, 47.7 ± 3.96; l_{18}, 54.0 ± 4.91.
l_1 with: *cm*, 48.9 ± 7.81; a_1, 50.5 ± 5.16.
c with: *pi*, 35.8 ± 10.2; *cm*, 47.3 ± 11.3; *z*, 50.0 ± 14.2.
ms_1 with: l_{18}, 40.8 ± 11.35.
sr with: *z*, 37.8 ± 9.56.
rb with: *cm*, 39.2 ± 9.03.

Summary

Twenty-two loci in lima beans were screened for linkages, 90 of 210 possible paired combinations having been tested for independent segregation in families derived from heterozygous plants by selfing. Ten linked combinations were found, which, combined with four linkages previously known, can be arranged in four linkage groups, as follows:



The correct order of l_{18} in (1) and l_2 and l_{16} in (3) has not been established.

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INTERSTELLAR MIGRATION AND THE POPULATION PROBLEM

GARRETT HARDIN*

ANYONE who discusses population problems with lay audiences is, sooner or later, confronted with questions of this sort: "But why worry about overpopulation? Won't we soon be able to send our surplus population to other planets?" It is not only the audience that adopts this point of view; sometimes the lecturer does, as appears from an Associated Press dispatch of 6 June 1958. Monsignor Irving A. DeBlanc, director of the National Catholic Welfare Conference's Family Life Bureau is reported as favoring such mass migration, "deploring an often expressed idea that birth control is the only answer to problems created by a fast-growing world population."

Neither physicists nor professional demographers have, so far as I know, recommended extra-terrestrial migration as a solution to the population problem, but the idea appears to be gaining ground among the laity even without scientific support. The psychological reasons for embracing this idea are two. On the one hand, some Roman Catholics welcome it because it appears to offer an escape from the dilemma created by the Church's stand against "artificial" methods of birth control. On the other hand, citizens of all churches worship the new religion called Progress, of which Jules Verne is the prophet. In this religion all things are possible (except acceptance of the impossible). Who is to set limits to Science (with a capital *S*)? Yesterday, the telephone and the radio; today, television and ICBM's; and tomorrow,—Space!—which will solve all our earthly problems, of course.

This is heady stuff. Strictly speaking, since it springs from an essentially religious feeling and is non-rational it cannot be answered by a rational argument. Nevertheless, for the sake of those bystanders whose minds are still open to a rational analysis it is worthwhile reviewing the facts and principles involved in the proposal to solve the population problem by interplanetary travel.

The Cost of Space Travel

It now seems possible that, before the century is out, manned landings may be made on Venus or Mars, with the establishment of temporary quarters thereon. But all evidence points to the unsuitability of these, or any other planets of our sun, as abodes for *Homo sapiens*. We must, therefore, look beyond the solar system, to other stars for possible planets for colonization.

The nearest star is Alpha Centauri, which is 4.3 light-years away. How long would it take us to get there? The rockets that we are now planning to send to the moon will have a maximum velocity in the neighborhood of 10 kilometers per second, or about 19,000 miles per hour. This may sound fast. But a body travelling at such a speed towards Alpha Centauri (which is 4.07×10^{13} kilometers distant) would require 129,000 years to reach its destination. Surely no one believes that a fleet of space ships with so long a transit time would solve our explosive population problem. The question is, then, what is the probability of improvements in space travel that would significantly cut down the time required to make such an interstellar journey? In trying to answer this question I have relied on an analysis by L. R. Shepherd[1], to which the interested reader is referred for technical details.

Shepherd presumes a technology in the release and utilization of nuclear energy that may take several centuries to achieve. To give the worshippers of Progress the maximum advantage we will assume that such an advanced technology is available *now*, and see how long it would take to travel to the near-

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est star. Using fantastically optimistic assumptions, Shepherd calculates that it might be possible to make the transit in a mere 350 years. The average speed of the trip would be about 7,000,000 m.p.h., though the maximum speed would be somewhat more, since 50 years would be required for acceleration at the beginning of the trip and another 50 years for deceleration at the end. (In passing, it should be noted that acceleration is more of a limiting factor than is velocity.)

To evaluate interstellar migration as a population control measure we must examine its economics. Here the unknowns are obviously great, but from data assembled by A. V. Cleaver[2] it appears that the foreseeable cost of a rocket ship could hardly be as little as $50 a pound, assuming economies of mass production and allowing nothing for research and development costs. How many pounds of ship would be required per man? Since we have no data on such a spaceship, let us borrow from our knowledge of atomic submarines, which are perhaps not too dissimilar. A spaceship designed to be self-maintaining for 350 years could hardly be less complicated or less bulky than an underwater craft capable of operating away from its depots for only a month or two. According to a news release[3] the submarine *Seawolf* weighs 3,000 tons and carries 100 men, a burden of 60,000 lbs. per man. A spaceship of a similar design, at $50 a pound, would cost $3,000,000 per man travelling in it. Would this be a reasonable cost for solving the population problem? Those who propose such a solution presume, or even recommend, that we do not alter our present reproductive habits. What would it cost to keep the population of the United States fixed at its present level by shipping off the surplus in spaceships?

According to a recent estimate of the U. S. Bureau of the Census[4] our population is increasing by about 3,000,000 people per year. To ship this increase off to other planets would, on the above conservative assumptions, cost about 9,000 billion dollars per year. The Gross National Product is now nearly 450 billion dollars per year. In other words, to solve our national population problem by this means we would, then, have to spend 20 times as much as our entire income on this purpose alone, allowing nothing for any other use, not even for food. It would surely be unrealistic to suppose that we shall do this in the near future.

Another aspect of the population problem is worth commenting on. Many philanthropically minded citizens feel that it is an obligation of the United States to solve the population problems of the entire world, believing that we should use the riches produced by our technology to make up for the deficiencies in luck or foresight of other peoples. Let's examine the economics of so doing. According to a recent estimate[5] the population of the world is increasing at a rate of 123,000 per day. To remove one day's increment by the postulated spaceship would cost about 369 billion dollars. In other words, we Americans, by cutting our standard of living down to 18 percent of its present level, could in *one year's time* set aside enough capital to finance the exportation of *one day's increase* in the population of the entire world. Such a philanthropic desire to share the wealth may be judged noble in intent, but hardly in effect.

In passing, it should be noted that we have so far made no mention of certain assumptions that are of critical importance in the whole picture. We have assumed that our nearest star has planets; that at least one of these planets is suitable for human habitation; that this suitable planet is uninhabited—or, if inhabited, that the humanoids thereon will gracefully commit suicide when they find we need their planet for our *Lebensraum*. (The tender feelings that would make impossible the control of reproduction on earth would presumably not interfere with the destruction of life on other planets.) Should Alpha Centuari have no planet available for migratory earthlings, our expedition would presumably set out for an even more distant star, perhaps eventually becoming a latterday interstellar Flying Dutchman.

Paradoxes of Space Emigration

Cogent as the economic analysis of the problem is, it does not touch on issues that

are of even greater importance. Consider the human situation on board this astronautical Mayflower. For 350 years the population would have to live under conditions of complete sociological stasis, the like of which has never been known before. No births would be permitted, except to replace the dead (whose substance would, of course, have to be returned to the common stores). Marriages would certainly have to be controlled, as would all other social interactions, and with an iron hand. In the spaceship, Progress would be unendurable. The social organization would have to persist unchanged for 10 generations' time, otherwise there would be the risk that some of the descendants of the original crew might wish to change the plans. It would be as though the spaceship had to set sail, so to speak, under Captain John Smith and arrive at its goal under President Eisenhower, without the slightest change in ideas or ideals. Can we who have so recently seen how fragile and mutable a flower Education is suppose that we could set up so stable a system of indoctrination? Paradoxically, only a people who worship Progress would propose to launch such a craft, but such worshippers would be the worst possible passengers for it.

Those who seriously propose interstellar migration as a solution to overpopulation do so because they are unwilling to accept the necessity of consciously controlling population numbers by means already at hand. They are unwilling to live, or to admit living, in a closed universe. Yet—and here is the second paradox—that is precisely the sort of universe the interstellar migrants would be confined to, for some 10 generations. Since the present annual rate of growth of the world's population is about 1.7 percent[6], by the time the first ship arrived at its destination, the whole fleet of spaceships enroute would enclose a total population six times as large as that still present on the earth. That is, in attempting to escape the necessities of living in a closed universe, we would confine to the closed universes of spaceships a population six times as great as that of the earth.

Moreover, there would be a differential element in the emigration from the mother planet. The proposal to emigrate is made by those who, for religious or other reasons, are unwilling to curb the reproductive proclivities of mankind. But not for such as these is the kingdom of a spaceship. They must stay behind while the ship is manned by those whose temperament creates no need for emigration. The reproductively prudent would be exiled from a world made unbearably crowded by the imprudent—who would stay home to perpetuate the problem into the next generation. Whether the difference between the two groups is basically biological, or merely sociological, would not matter. In either case, natural selection would enter in. The end result of this selective emigration would be to create an earth peopled only by men and women unwilling to control their breeding, and unwilling, therefore, to make use of the very means they propose to escape the consequences.

The proposal to eliminate overpopulation by resort to interstellar migration is thus seen to yield not a rational solution at all. The proposal is favored only by men who have more faith in gadgetry than they do in rationality. Should men of this temper prevail, and should the gadgetry prove equal to the quantitative demands put upon it, the result would nevertheless be the ultimate production of a world in which the only remaining controls of population would be the "misery and vice" foreseen by Malthus 161 years ago.

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THE PROBLEM OF SUPERFETATION IN THE MOUSE

W. F. HOLLANDER*

AMONG a large number of breeding control mice killed when pregnant for an X-ray experiment at this laboratory, one has presented an intriguing aberration, at first diagnosed as superfetation. The mother was of a moderately inbred "ruby belted" strain; she had been continuously with a male, and was nursing a previous litter about two and a half weeks old.

What attracted attention was the presence of a very large fetus in the midst of a number of small ones. Comparison of this giant with the others showed that developmentally it was much advanced over them. It had an external ear, distinct digits on the limbs, good muscle development, and hair follicles in the skin. The other fetuses lacked all these, and may be described as being in the late limb-bud stage. The difference corresponds to about four days' growth in the mouse, or the same as the length of the oestrus cycle. It seemed logical to assume that the older fetus came from one ovulation period, and the younger fetuses from a second period.

Superfetation is defined as "conception during pregnancy", the result of a second batch of eggs being ovulated from the ovary and fertilized before the previous batch finishes gestation. It has no relation to "superovulation", a very large number of ova released at one time. This has been induced experimentally by injection of anterior-pituitary hormones, and can result in "super-pregnancy". Superfetation should also not be confused with "superfecundation", where two or more males contribute to fertilization of the eggs from one ovulation period[5].

INTACT UTERUS

Figure 7

Ventral view of uterus, showing the position of the large fetus in the right horn. The three embryos in this horn between the large one and the vagina are resorbing (recently dead).

Discussion

Several apparently authentic cases of superfetation are on record for mice. Gates[4] reported that a Japanese waltzer, which had been separated from the male before parturition, had two litters nine days apart (three young in each litter). Similarly, Stowell[8] isolated a pregnant female a few days before a litter of six was born. Another litter of eight young appeared 16 days after the first. Bloch[2] had an almost identical case, a first litter of four, and a second of eight after 16 days. Dr. Sally L. Allen[1] of the University of Michigan reported a female, isolated shortly after birth of a litter of five, which had a second litter of five after eight days.

Rollhäuser[6] killed a female two days after observing a copulation plug in the vagina, and discovered that she had already been pregnant over a week, with seven embryos implanted in

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FETAL CONTRASTS

Figure 8

The uterus has been opened to reveal the fetuses, and their membranes removed. The smaller fetuses are about four days behind the larger one in developmental stage.

the uterus. Examination of the ovaries revealed that in addition to large corpus luteum development from the earlier ovulation there had been fresh ovulation, and eggs were found in the Fallopian tubes. Bloch[2] observed that pregnant female mice often copulate and show vaginal plugs, but none of these in her experience produced superfetation. She notes that the uterus is blocked by the implantation processes for some days, so that sperms could not then reach the eggs (if any).

In other kinds of mammals, including man, many cases of superfetation have been observed (*cf.* bibliographies in Bloch[2] and other cited papers). Shackelford[7] suggests that in the mink superfetation may be considered normal. A second mating a week or more after the first induces a second ovulation. By using different males with suitable genetic markers the progeny can be distinguished. However, because of delayed implantation, all the young from successive ovulations are "equalized" in developmental stage and are born at the same time.

The phenomenon of delayed implantation[3] is not limited to the mink. It is well known also in the mouse and rat, but normally occurs only if the female is suckling a previous litter. Bloch[2] notes that by giving the female additional young to nurse, implantation can be delayed as much as three weeks—as long as the entire course of ordinary pregnancy. Meanwhile the embryos are in a state of arrested development as blastocysts, free in the anterior portion of the uterus.

That delayed implantation could be important in interpretation of superfetation was pointed out by Weichert[9]. He discovered a rat pregnancy much like the one here reported in the mouse. The female had a previous litter of nine young which she was nursing, and her mate had been removed the day after postpartum mating. She was killed when the young were a month old. One fetus was about four days ahead of the remaining four in stage of development. Since superfetation is impossible here (unless sperms survived much longer than ordinary), Weichert proposed the explanation that irregular delay in implantation had occurred. He also[10] demonstrated that female hormone (stilbestrol) provided to the nursing female makes the uterus receptive to implantation without delay.

The close similarity of the present case to Weichert's[9] makes it seem likely that irregular delay of implantation is the best explanation here also. If superfetation were involved, one would expect the implantation delay to equalize development, rather than to leave the embryos different. Moreover, although ovulation could well occur during pregnancy, it would probably be suppressed by the endocrine situation involved in lactation. The answer is not final, however, and superfetation remains as a possible interpretation.

Summary

A female mouse, pregnant and nursing a 2½-week-old litter, was killed and found to have 11 fetuses of which one was about four days older developmentally than the others. Review of pertinent literature indicates that this is probably a case of irregular delay of implantation rather than superfetation.

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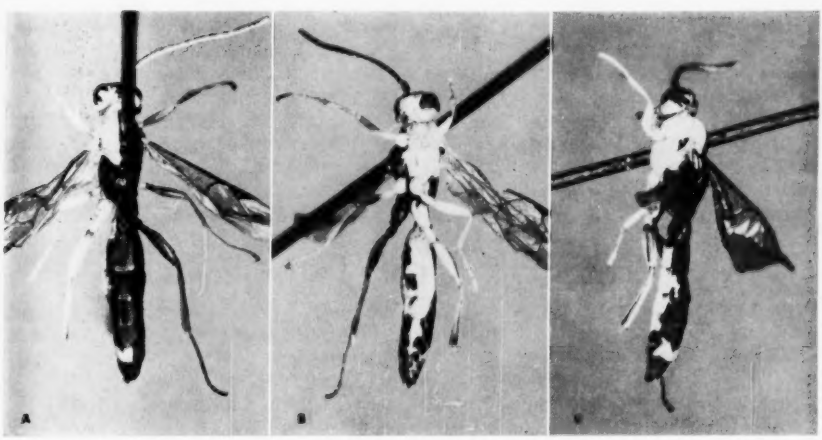
AN ALBINO MOSAIC IN HYMENOPTERA

(*Phaeogenes hariolus* Cresson: Ichneumonidae)

W. R. M. Mason*



ALBINO MOSAIC

Figure 9

Albino mosaic of *Phaeogenes hariolus* Cresson. *A*—Dorsal aspect; *B*—Sinistroventral aspect; *C*—Sinistral aspect.

Among specimens recently submitted to me for identification is a strangely colored male of *Phaeogenes hariolus* Cresson, a hymenopterous parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.). This specimen is a perfectly normal male externally in all respects except color.

In the normally colored male of *P. hariolus* the body is black with the following parts yellow: mouth parts, face, clypeus, sometimes underside of scape, tegula, wing base, subtegular ridge, humeral angle of pronotum, ventral side of abdomen except the laterosternites and posterior sternites and genitalia. The four

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anterior coxae and trochanters are yellow; the remainder of these legs red. The hind coxae and trochanters are black; the remainder of the hind legs varying from red to black.

In the mosaic albino (Figure 9), the black and red coloration is extensively replaced by yellow, but mostly on the left side of the body and legs.

In addition to the normal yellow markings, the following parts of this insect are yellow: lower part of both antennae, left side of frons, left cheek, most of left temple, left occipital region, entire postoccipital region, large part of upper right temple, right cheek immediately above mandible, prosternum, all of left propleuron, and central half of right propleuron, central part of pronotum and entire left side of pronotum, left side of mesoscutum and scutellum, left mesopleuron, left mesosternum and left prepectus, small areas in center of right mesosternum and right prepectus, most of the left metapleuron, most of left side of petiole, small part of left side of third tergite, entire left side of sixth tergite, small areas on both sides of seventh tergite, left side of eighth tergite, second to fifth left laterosternites, left side of hypogium, base of left paramere, lower part of right side of seventh and eighth tergites, left front and middle legs entirely, left hind coxa except for two or three small black streaks, left hind trochanter, left hind femur and tibia, except for two or three reddish streaks, left hind tarsus above, left parastigma and a few vague markings on left stigma.

Mr. D. R. Macdonald (in litt.), Forest Biology Laboratory, Fredericton, New Brunswick, who submitted the specimen, wrote, "The spruce budworm host was collected July 15, 1955, near Middle Brook fire tower, Balmoral Twp., Restigouche Co., New Brunswick. The parasite emerged on July 28, 1955, and is the only aberrant specimen recovered in six years of rearing. During this time we have recovered over 320 *P. hariolus* from 85 plots in the northern part of the Province."

The specimen is preserved in the Canadian National Collection, Department of Agriculture, Ottawa.

DROSOPHILA COUNTER

GEOFFREY KEIGHLEY AND E. B. LEWIS*

IN some types of investigations with the *Drosophila* fly large populations are reared. Frequently it is impractical to count the flies by hand, yet the total number examined must be determined with some accuracy. For example, in mutation studies many thousands are often examined individually in order to identify rare mutant types. After the mutant types have been removed the remaining flies are no longer needed but must nevertheless be counted in order to estimate the mutation frequency. An automatic means of counting such populations has therefore been devised.

If quantities of flies are tumbled or shaken in a variety of ways, instead of separating or lining up which would make them easier to count, they tend to hang together and accumulate in masses. They are easily broken or crushed. Because of size differences enumeration by weighing is unreliable. Although sampling techniques can be employed, it is difficult to insure that sampling is at random. We find that they can be suspended in water and counted with sufficient accuracy in a hydraulic system.

Description

After a population of living, etherized flies has been examined and any desired types removed for further breeding, the remaining flies are killed and stored in detergent-fixative solution consisting of 5 percent tri-thiol-sulfonate (available as TTS from F. C. Nash Co., Pasadena, California) and 10 percent acetic acid in water. The flies should remain in the detergent-fixative at least several days in order to insure good penetration of the detergent. The detergent is essential and serves to prevent the flies from floating or clumping together. The acetic acid is merely a convenient preservative. They should be kept covered at all times to keep out live flies and to prevent evaporation. Flies will then remain well preserved indefinitely.

The apparatus, Figure 10, consists of three flasks which are joined together by tubing to make a system which is open only at the input and output ends. Approximately 250 ml of a dense suspension of flies in detergent-fixative are put into the first cylindrical flask 1, about half filling it, and the flask is clamped, 2, to the rest of the system. The flies are stirred slowly (75 RPM) by a paddle, 3, driven from the outside through seal, 4. Cold tap water to run the counter is put through the following, which are not shown in Figure 10: a 3-way valve with a waste bypass, a pressure relief valve, a wire gauze strainer, a ceramic filter, an adjustable pressure regulator, a pressure gauge and a bubble trap. This water enters the system at 13 and can be added to the first flask through one or both of two inlet branches, 5 and 6. These have different sized small bore capillaries in them which limit the flow and each is controlled by a screw clamp, 7. Water is started through the most restricted branch at such a rate that flies leave the flask through the submerged outlet at about 7-10 per second. In this first flask the flies are stirred to keep them evenly distributed, there is some dilution, and they are then removed at a controlled, more or less constant rate to a 100 ml round bottom boiling flask, 8.

In this second flask more water is added through a jet, 9, which further dilutes the flies and breaks up clumps. Through another submerged outlet tube the flies and water flow into a 3 neck, 100 ml, round bottom flask, 10. Again more water is added through two jets to stir and dilute. The flies finally leave through the vertical capillary tube, 11, which is about 0.065 in. inside diameter. The funnel-shaped mouth of the capillary is crossed by one of the jets. On their

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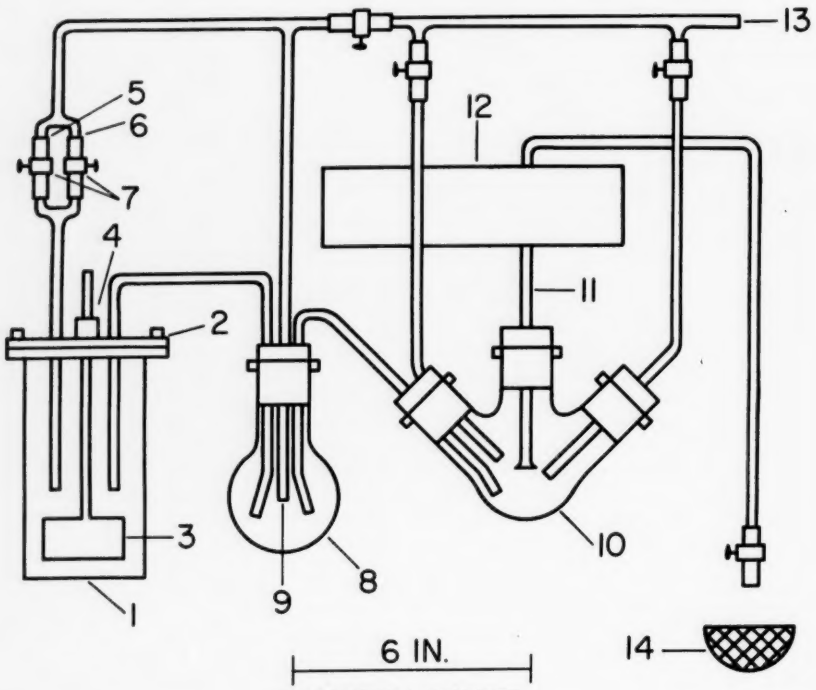

Figure 10

Schematic diagram of the fly counter. The power supply, pulse amplifier and pulse counter are not shown.

way up the capillary the flies traverse the box, 12, where they interrupt a focussed beam of light and produce a signal in a phototube. A fine screen, 14, under the outflow collects the flies and lets the water waste to a sink. The water flow at the outlet is about 500 ml/minute.

The phototube pulses are amplified, and shaped in a discriminator circuit. They can be counted in a scaler of the kind used for radioactivity measurements.

After the apparatus has been charged with a batch of flies and counting has started it needs little further attention. When only a few flies are left in the first flask they can be swept out quickly by increasing the flow of water.

Debris, such as food particles or parts of flies, may be present. Nearly all of these unwanted objects give smaller phototube pulses than do flies. By proper setting of the amplifier gain these pulses can be kept so small that almost none will trip the discriminator, but without resulting in any significant loss of fly counts. To do this reliably both the amplifier-discriminator and the phototube exciter lamp are run from regulated power supplies. Not only must the amplifier gain be set initially at the proper point, it must be possible to make a routine check of the sensitivity. We have found the following method convenient. Through a hole in the side of box 12 a piece of wire is held at right angles to the capillary and touching it on the side facing the exciter lamp. The wire is moved smartly up and down across the beam of light and pulses then come from the phototube. The size of the pulses depends on the size of the wire. After the

amplifier setting has been determined it is easy to pick two sizes of wire, one of which should produce pulses barely large enough to trip the discriminator over a small range around this setting, and one which will not. This checks the system from light to output pulse and counter, and will show up any considerable changes in sensitivity. Other methods which have been devised for testing and adjusting particle counters are not suitable for use with flies[1].

Counting Performance

Counting performance has been tested in several ways. Although the counter mixes and greatly dilutes the fly suspension it is obvious that two or more flies can sometimes count as one. Hence the observed count will tend to underestimate the true number present. This systematic error has been empirically determined by collecting batches of approximately 10,000 flies which have gone through the counter at relatively high rates (over 15 flies per second) and at a measured and nearly constant rate of counting per batch. Such batches are most easily collected by introducing a very large supply of flies, 50,000 or more, into flask 1. A number of batches of about 10,000 can then be drawn off at a more or less fixed rate of flow per batch by careful regulation of the clamps on 5 and 6. The rate of counting is measured with a stop watch while the batch is being collected. Each of the batches is then recounted at a slow rate of four per second or less. In a test of six batches of approximately 10,000 flies each the following relationship held true. The difference between the counts from the slow and fast runs when expressed as a percentage of the count from the slow run is roughly equal to the quotient obtained by dividing the fast rate of counting, expressed in flies per second, by 10. For example, at the fast rate of about 20 flies per second the difference between the count obtained at the slow rate and that at the fast rate was about two percent of the total count at the slow rate; while at 120 flies per second the corresponding difference was about 12 percent. The counter is run ordinarily at a maximum rate of about seven to 10 flies per second. This insures reasonably accurate counting. If the counter is run at rates above about 10 per second or at water pressures much above 8 lbs. appreciable breakage of the flies may occur.

A batch of 300 heads of flies was repeatedly run through the counter at different gain settings. At the gain setting used for counting flies, the batch was run through three times; the total counts observed for these runs were 2, 1 and 8. In the latter case it was observed that clumping of the heads was responsible for some of the eight counts.

Males seem to be the best test objects for repeated runs. Females begin to show appreciable breakage after five runs. Pupae tend to clog the capillary tube. Seeds break up. It is difficult to find plastic balls of the right density. A batch of 1,000 males was counted 10 times. With the rate of counting held in each run to four flies or less per second, counts on the 10 runs ranged between 996 to 1,000.

Normally each batch of flies is counted twice. The difference between the first and second counts has been calculated for an unselected series of 40 batches of flies varying in number between 1,000 and 30,000 flies per batch. The magnitude of this difference for a given batch was in no case over 1.3 percent of the average of the two counts for that batch.

Summary

An apparatus is described for counting large numbers of *Drosophila* flies. The flies are killed and stored in a detergent-fixative solution. They are then put into the first of three connected flasks. Water is added and as the flies move through the flasks they are diluted and violently agitated by streams of water. They leave the last flask through a capillary and are counted by a photocell. The counting equipment is able to discriminate against contaminating particles. Counting performance is adequate and can be controlled. Tens of thousands of flies can be counted in a day with a minimum of attention.

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SOME X-RAY INDUCED MUTANTS IN THE CARNATION

Dianthus caryophyllus

YONEO SAGAWA AND GUSTAV A. L. MEHLQUIST*

IN recent years, a variety of plants in the vegetative phase of the growth cycle have shown changes in growth habit[2], color and russetting of the skin of fruits[3,4,7], form and color of leaves and flowers[2,5,7,9,12,13,15,16] and the time of maturity of the fruit[2] after exposure to ionizing radiations. This report deals with some radiation-induced mutants involving doubleness and male fertility derived from treatment of vegetative propagates of three clones of the greenhouse carnation, *Dianthus caryophyllus*.

Materials and Methods

Although these mutants were observed during the course of experiments designed for other purposes, the occurrence of several such mutants and their significance indicated that they are worthy of special consideration. Rooted vegetative propagates from the semi-double, red-flowered seedling clone, William Sim, and two of its spontaneous flower color variants, Pink Sim and White Sim, were established in pots. The terminal portion of each shoot was removed to promote the development of lateral branches and thus provide a large number of shoots for treatment. In 1954 whole plants were irradiated with a single acute dose of 2500 r or 5000 r of X-rays. Each treatment consisted of nine plants per clone; three plants of each clone served as controls. The number of control plants was small because extensive data was available on the behavior of these clones under commercial cultivation and showed them to be very stable. In 1956 only the clone White Sim was utilized. The treatment group consisted of 10 controls and 16 plants exposed to 5000 r of X-rays. The shoots ranged in length from 0.2 to 16.0 cm. at the time of irradiation. The exposures were made with a G. E. Maxitron X-ray Machine which was operated at 250 kv., 30 ma. with 1 mm. of aluminum filtration, and a dose rate of approximately 400 r per minute. The distance from the target to the object was approximately 50 cm. The irradiated plants were grown in the greenhouse and the flowers were scored when the plants came into bloom three to eight months later. The branches at flowering ranged from 38 to 134 cm. in length.

Results and Discussion

Doubleness

The commercial or standard greenhouse carnation has from 30 to 60 petals and has been classified as semi-double because it is known to be genetically heterozygous for the factor governing doubleness. The single carnation generally has five petals although a few exceptions have been noted with four or six petals. The fully double or bullhead, as it is often known commercially, has from 100 to 350 petals, bursts its calyx in opening and usually fails to set seeds. The frequency of mutants involving petal number induced by treatment of semi-double clones with X-rays is shown in Table I. The data indicate that treatment with 2500 r of X-rays was not effective in producing mutants. Three out of 129 branches or 2.3 percent of the branches bearing flowers after treatment with 5000 r resulted in single flowers. Figure 11 illustrates a plant of the clone White Sim on which one branch has been induced to produce single flowers after treatment with 5000 r in 1956. The branch in the center of the photograph has flowers with five petals while the one on the right has normal semi-double flowers with 30 to 60 petals.

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X-RAY INDUCED SINGLE-FLOWERED MUTANT

Figure 11

A single-flowered branch (left) induced after treatment of White Sim with 5000 r of X-rays in 1956. The branch on the right shows the normal semi-double flowers. ca. × ¼.

Singleness in the carnation is a monogenic character and incompletely recessive to doubleness while the heterozygote yields semi-double flowers[1,6,8,11,14]. The dominant gene for doubleness has been designated as *Da* by Imai[8]. Since the clones under study were known to be semi-double and thus heterozygous for the factor governing doubleness (*Da*/+), it can be postulated that the single flowers are the result of a chromosomal deletion, a loss of a whole chromosome or a point mutation of the factor governing doubleness. Experimental evidence to distinguish the possible mechanism for these changes is currently being sought through cytological studies of the somatic chromosome number and behavior at meiosis of the mutants and by crossing them with recessive stocks.

Male fertility

William Sim and its flower color variants are generally male sterile, producing only an occasional fertile anther. The two single mutants derived from treatment of the clone, White Sim, were male sterile but the one (R-1-5) derived from William Sim proved to be male fertile. Induced male fertility has been found to occur independent from induced singleness by Mehlquist and Sagawa[10]. A plant of William Sim exposed to gamma radiation in the Brookhaven National Laboratory Gamma Field at the rate of 135 r per 20 hour day for 113 days in the summer of 1953, after removal from the field, produced one branch which bore fertile, semi-double flowers. Subsequent propagation of this branch has shown that this is a stable change. The independent occurrence of induced singleness and induced male fertility indicate that the one plant (R-1-5) derived from William Sim is the result of two independent mutations within a single cell. The attainment of a single-flowered male fertile mutant of William Sim is of practical significance to the further development of this organism since this seedling possesses many desirable characteristics which could not be readily studied or utilized for further development because of the paucity of functional pollen.

Summary

Three single-flowered mutants were induced upon exposure of vegetative propagates of three semi-double flowered clones of the greenhouse carnation, *Dianthus caryophyllus* cultivars William Sim (red), Pink Sim and White Sim to 5000 r of X-rays. Although these clones are usually male sterile, the single-flowered mutant (R-1-5) derived from William Sim was found to be male fertile. Evidence is given to indicate that the male fertile, single-flowered plant (R-1-5) is the result of two independent mutations. Further experimental data are being sought to establish the nature of these mutations.

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TABLE I. Frequency of mutants involving petal number induced by treatment of semi-double flowered clones

Clone	Year	Treatment	No of shoots treated	No. of branches with flowers	Flower types	
					Semi-double	Single
Wm. Sim	1954	Control	13	7	7	0
Pink Sim	"	"	8	6	6	0
White Sim	"	"	10	7	7	0
White Sim	1956	"	41	26	26	0
Totals:		Control	72	46	46	0
Wm. Sim	1954	2500 r	42	31	31	0
Pink Sim	"	"	44	33	33	0
White Sim	"	"	48	34	34	0
Totals:		2500 r	134	98	98	0
Wm. Sim	1954	5000 r	45	28	27	1
Pink Sim	"	"	46	33	33	0
White Sim	"	"	56	29	28	1
White Sim	1956	"	67	39	38	1
Totals:		5000 r	214	129	126	3

LINKAGE OF BRACHYPODISM

A New Member of Linkage Group V of the House Mouse

MEREDITH N. RUNNER*

A RECESSIVE mutation for brachypodism in the house mouse was described by Landauer[5] who kindly supplied us with some homozygous, brachypod animals. The symbol *bp* has been assigned to this gene.

Classification of brachypod animals has never offered any uncertainty since approximations of normal feet were never seen in brachypod mice. Brachypodism was combined with animals expressing other morphological mutants, fused, tailless (Tt^1) and undulated, with no apparent modification of the brachypod phenotype. Unlike the short footedness described by Hardy and Strong[4], penetrance of brachypodism was assumed to be 100 percent. Backcross matings with a multiple recessive stock indicated that brachypodism and the agouti locus failed to dissociate. Since the stock carrying brachypodism was already carrying wild type *A* at the agouti locus, the gene for dominant yellow was subsequently used for establishing linkage or identity by attempting to determine the recombination frequency between brachypodism and the yellow (A^y) locus. Backcross, coupling type matings $+A^y/bp+ \times bp+/bp+$ gave 287 young (Table I) of which one animal or 0.35 percent was a recombinant, $A^ybp/+bp$. An unusually close linkage between brachypodism and the agouti locus was thereby demonstrated.

TABLE I. Backcross segregation of yellow and brachypodism

Parents		Phenotype of progeny			
♀	♂	$bp+$	$+A^y$	bpA^y	$++$
$\frac{+A^y}{bp+} \times$	$\frac{bp+}{bp+}$	83	82	1	0
$\frac{bp+}{bp+} \times$	$\frac{+A^y}{bp+}$	70	51	0	0
Total		153	133	1(0.35%)	0

The foregoing data demonstrate linkage and nonidentity but do not indicate on which side of the agouti locus the gene for brachypodism lies. The known location of *A* between kreisler, *kr*, and undulated, un^2, permits either of two positions for *bp* as follows:

kr 3 · *A* 5 *un*

(a) (b)

The recombinant, *bp* A^y (Table I), enabled us to test the repulsion phase for the two possible positions (a) or (b) by means of the following type of mating:

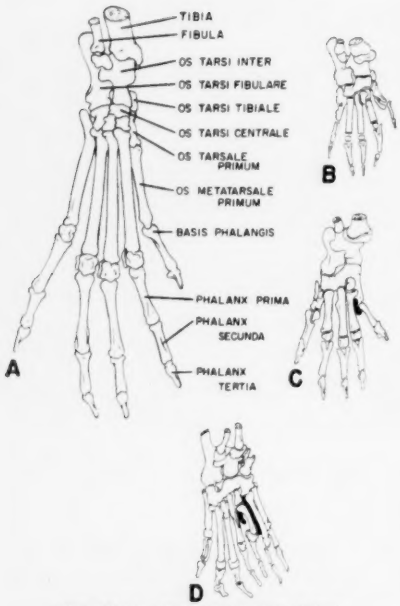
(a) $\frac{bp\,A^y+}{++\,un}$ (♀) $\times \frac{bp+\,un}{bp+\,un}$ (♂) or

(b) $\frac{A^ybp+}{++\,un}$ (♀) $\times \frac{+\,bp\,un}{+\,bp\,un}$ (♂)

If *bp* lies on the far side of agouti from *un*, position (a), then a single break between *bp* and *A* will separate *bp* and *un* so that they will segregate into different gametes. If on the other hand *bp* lies between *A* and *un*, position (b), then a single crossover between the *A* and *bp* will result in *bp* and *un* remaining linked within the same gamete. Observations presented in Table II demonstrate that *bp* segregated independently of the segment A^y+ on two separate occasions, thereby excluding position (b) insofar as single recombinations are concerned.

Since relevant recombinations were observed only twice, the potential sources

*Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine. This investigation was supported by a research grant (G-5300) from the National Institutes of Health, Public Health Service, U. S. Department of Health, Education and Welfare.



NORMAL, BRACHYPOD AND POLYDACTYLOUS FEET

Figure 12

Drawings of the dorsal surface of hind feet made from alizarin-stained preparations (× 3). *A*—Normal right hindfoot. *B*—Right hindfoot of brachypod animal 20 days old. *C*—Right hindfoot of brachypod animal 50 days old. *D*—Polydactylous and brachypod foot photographed in Figure 13.

of error must be carefully assessed. If position (b) were held by brachypod, the recombinants observed could possibly have been obtained by double crossing-over. The expected frequency of such an occurrence would be 0.05 × 0.0035 or 0.000175 and the probability of two occurrences of simultaneous crossing-over both between *bp* and *A* and between *A* and *un* would be less than one in 1,000. Any additional effect of interference within such a short segment would further reduce the probability of double recombinants and therefore of position (b) for brachypodism. Position (b) is thereby excluded.

The frequency of recombinations in Table II, 0.296 percent is similar to 0.35 percent observed in Table I. Combining data in Table I and Table II, the 962 animals yielded a frequency of 0.312 percent for recombinations between agouti and brachypodism. Of the approximately 85 loci known for the mouse only one pair of loci, *d* and *se* is reported[3] to have a recombination value lower than that for *A* and *bp*. The location of brachypodism close to the agouti locus brings the total known loci in linkage group V up to 12 and renders this gene of little use as a marker for linkage studies. Possibly those interested in physiological genetics at the agouti locus could use a morphological marker gene that is closely linked and permits identification of genotype well before pigmentation becomes apparent.

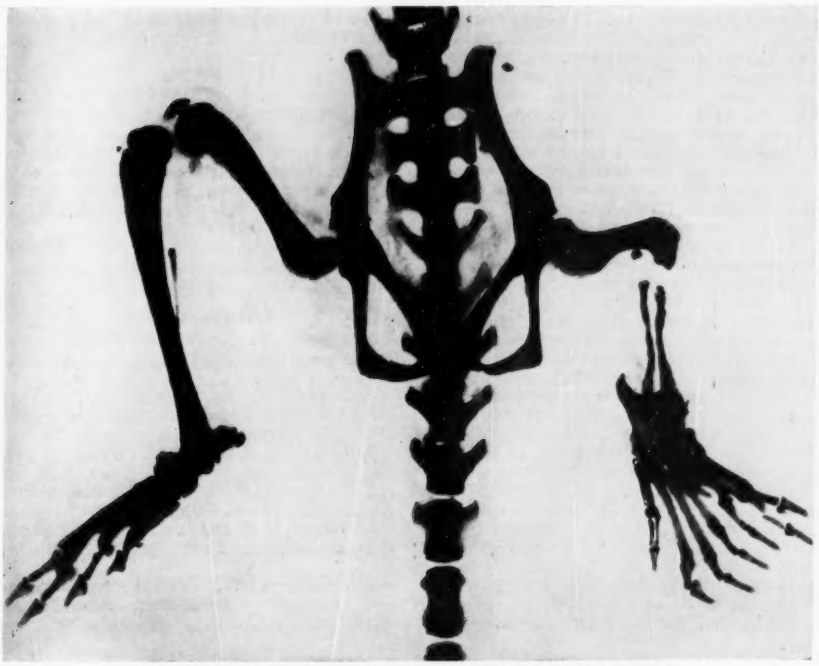
Discussion

The tripoint linkage test has also provided data for recombinations between agouti and undulated. Previously, Carter[1] reported a frequency of 3.86 percent and Fisher[2] reported 4.62 percent. The latter author found a correlation with age, leading to recombination frequencies between agouti and undulated that ranged from two to seven percent. The recombination frequency of 4.7 percent for *A* and *un*, Table II, falls well within these limits and thereby confirms observations of previous investigators.

Since the description of brachypodism was published[5], reduced feet in mice, brachydactylia, was reported by Hardy and Strong[4]. Unlike brachypodism all bones of the foot were present and normal in shape except for the shortened phalanges. The phalanges, not bifurcated as in brachypodism, primarily accounted for the short footedness. Comparative measurements indicate the short footed mice of Hardy and Strong (adjusting for an apparent typographical error where *mm* should

TABLE II. Tripoint repulsion data for yellow, brachypodism and undulated

Parents	$\frac{bp\ A^y\ +}{+\ +\ un}$ (♀) × $\frac{bp\ +\ un}{bp\ +\ un}$ (♂)	
Phenotype of progeny	Number of progeny	Recombination percent
bp A^y +	315	
+ + *un*	326	
bp A un	14	4.75 *A* and *un*
+ + +	18	
bp + *un*	1	0.296 *bp* and *A*
+ *A^y* +	1	
bp + +	0	0 double recombinants
+ *A^y un*	0	
Total	675	



MICROMELIC, POLYDACTYLOUS LIMB IN AN ANIMAL HOMOZYGOUS FOR BRACHYPODISM

Figure 13

Photograph of the ventral surface of an alizarin-stained preparation. The right foot shows brachypodism and the left limb shows brachypodism, micromelia and polydactylism.

read *cm*) to have hindfeet appreciably longer than those of brachypod mice. Supernumerary metatarsals were described by Hardy and Strong but this was not surprising since their short footed animals were found in a strain showing 75 percent penetrance of preaxial polydactylism. The 16 cases of short footedness were found among 491 offspring from nonbrachydactylous parents that had produced one or more short footed offspring. This 3.07 percent frequency indicated a "complex recessive" inheritance and showed brachydactylia to be genetically distinct from brachypodism.

The brachypod animals described by Landauer[5] were not polydactylous but in the *pes*, for example, a supernumerary bone occurred between the fourth and fifth digit on the flexor surface and between the third and fourth digit on the extensor surface of the foot. The former was interpreted as a duplicated metatarsal postaxially. Landauer described the small bones of the feet as present but somewhat reduced in size and irregular in shape and location.

Observations on our material confirm those of Landauer[5] on supernumerary bones of the foot, duplication of metatarsals, absence of phalanges and bifurcation of the basal phalanges. Considerable variability in detail, perhaps a result of differences in genetic background, was seen. Our material differed from the published description insofar as duplication of metatarsals usually occurred preaxially, tarsals were frequently fused, the fifth basal phalanx frequently had two parallel bones for all or part of the length, and the supernumerary bones on the extensor surface of the foot were unpredictable in number and location. Comparisons of *B* and *C* in Figure 12 with *A* demonstrate the difficulty with which one homologizes the bones of the brachypod animals with the normal. Supernumerary bones, fusions and missing elements often make classification of tarsals, metatarsals, and basal phalanges arbitrary if not impossible.

During the course of accumulating the linkage data, a single variant was observed that could not be ascribed to the genes under investigation. Description of this case of unilateral micromelia associated with polydactylism (Figure 12*D* and Figure 13) seems warranted both because of the modification of the expression of brachypodism and because I am aware of no report or previous observation of

micromelia in the mouse. The right rear limb is that of a typical brachypod animal and conforms to the above description. The left micromelic rear limb (Figure 13) has an abnormally short femur, even for brachypodism. The tibia and fibula are reduced to two filaments shorter than is normal for metatarsals. The metatarsals are reduced but not to the extent that is typical for brachypod animals. In addition to the micromelic features of this limb, it also displays polydactylism. The dual basal phalanx of a lateral digit is immediately apparent. An accessory metatarsal projecting between two digits (Figure 12*D* shaded) is typical of brachypod mice, but the supernumerary digits have been seen but once. Detailed examination of the bones of the foot shows typical fusions and irregularities in shape. Additional evidence of incipient postaxial duplication is seen on the raised ridges on the dorsum of the basal portions of the middle metatarsals. One metatarsal has a complete duplicate that lies directly behind (Figure 13*D*, shaded). The limb is so severely deformed that one hesitates to designate one side as pre- and another as postaxial. Irrespective of which designation is made the preaxial digit has one more phalanx than is typical of brachypodism. Furthermore the metatarsals of this foot are relatively longer than those of the opposite limb. The animal with micromelia and polydactylism has foot elements that are more like normal than is expected under the influence of the gene for brachypodism.

Summary

Brachypodism is located in linkage group V of the mouse between kreisler and agouti. The data showed 0.29 percent recombination between brachypodism and the agouti locus. A single instance of unilateral micromelia with polydactylism is described. The sequence of nearby genes in linkage group V and approximate recombination percentages are:

kr		*bp*		*A*		*un*
	3		0.3		5	

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TWO NEW DELETERIOUS MUTATIONS OF TRIBOLIUM CONFUSUM

DANIEL J. MCDONALD*

DESPITE the ease with which *Tribolium* can be reared in the laboratory, and the wealth of information available concerning its ecology[3], the genetics of these insects has received relatively little attention. Not more than five mutations have been described[2,4,5,6,7] and no systematic search for new mutations or attempts to induce them have been reported. For this reason, during the course of experiments involving the examination of several thousand individuals belonging to the *confusum* species, careful attention was given to the detection of any spontaneous mutations that might appear. This report is a description of two newly isolated mutations of more than routine interest which are now being used in a series of population studies. Both mutations modify viability, and one mutation is the first instance of a sex-linked semi-lethal to be found in *Tribolium*.

Results

The mutation "split"

The first mutation occurred in a wild strain of *Tribolium confusum* derived from a single pre-fertilized female captured in a feed bin containing rabbit pellets. An inbred line, propagated by brother-sister matings, was started from this strain, and produced among the offspring of the second generation a few unusual individuals. The elytra of these beetles were shortened to the extent of exposing the posterior third of the abdomen and each elytron was separated from the other along the midline by a space, creating the impression that the cuticle covering the dorsal surface of the abdomen was split longitudinally. The variants were isolated, but died within a few days and left no progeny. From the third inbred generation consisting of 81 individuals, 12 similar variants were obtained, and from their offspring a pure strain was started which has continued to breed true for the eyltral abnormality for over eight generations. Because of the unusual appearance of the elytra, the mutation has been designated "split" (symbolized *sp*).

It soon became obvious that the *sp* mutants suffered from reduced viability and were particularly susceptible to damage while being handled. During routine transfers, in which adults were brushed from one vial to another, it was not unusual to find the following day that over half the adults in the mutant cultures were dead. Normal beetles, by comparison, showed no signs of injury when treated in the same way. The problem of handling the mutants without affecting them adversely can be largely overcome by confining such operations to the pupal stage. The pupae seem hardier than the adults and, in addition, can be sexed more easily.

To resolve the problem of the inheritance of *sp*, pair matings were made between mutants and a wild type strain. A wild strain derived from the phenotypically normal siblings of the original mutants was used, for it was felt that its residual genotype would match most closely that of the mutant stock. Thus, possible complicating factors such as penetrance and dominance modifiers might be eliminated. The matings were made in vials containing 3 grams of a standard *Tribolium* medium, that is, a mixture consisting of 95 percent sifted whole wheat flour and five percent dried brewer's yeast. All cultures were incubated at 29±1° C and relative humidity 60-70 percent. Handling of the mutants was kept to a minimum and done, where possible, only during the pupal stage. While the age of the beetles varied to some extent, none was more than 10 days old at the time of mating.

The data from the F_1 and from an F_2 produced by mass mating the F_1 of each cross are summarized in Table I. Examination of these data indicates that split is due to a recessive autosomal gene. With one exception, cross A5, there were no split individuals in the F_1, and the F_2 data fit the expected 3:1 ratio of wild type to split quite closely. The most likely explanation for the appearance of split beetles in the F_1 of cross A5 is that the phenotypically normal parent was a heterozygote. The F_1 was about one-half wild type and one-half split, thus meeting the theoretical expectation for such a cross almost exactly. In view of the fact that the wild strain used for the crosses was derived from the same line which produced the mutants, it would not be surprising to find occasional heterozygotes in this strain. Crosses C1, C2 and C3 were included to demonstrate that penetrance seemed to be complete.

*Department of Biology, Dickinson College, Carlisle, Pennsylvania. This investigation was supported in part by research grant RG-5406 from the National Institutes of Health, Public Health Service, and by a grant-in-aid from the Sigma Xi-RESA Research Fund.

Further confirmation of the single gene hypothesis was obtained by backcrossing 67 F_2 individuals with the split strain. In nine of the 35 crosses producing offspring, the F_2 parent was split, and in each of these cases, as was expected, all of the offspring were mutants, too. Of the 26 wild type F_2 tested, 19 proved to be heterozygotes and seven were homozygous wild type. This ratio does not differ significantly from the expected 2:1 ratio of heterozygotes to wild type ($\chi^2 = 0.483$, $P = 0.50$).

It is interesting to observe that only 49 of the 83 pair matings made in the parental cross and the backcross were productive. The frequency of fertile matings, 0.59, is unusually low, for by comparison, the frequency of fertile crosses between wild type beetles taken from other stocks is rarely less than 0.95. This suggests that the fertility of the strains used in these experiments is considerably reduced, but whether this reduction is an effect of the *sp* mutation or of inbreeding cannot be determined from these data.

In view of the fact that inherited abnormalities which appear during inbreeding may sometimes depend for their expression on the degree to which the mutant strain is inbred[1], it seemed necessary to determine if *sp* fell into this category before using it in population studies. Accordingly, 44 pair matings were made between *sp* mutants and individuals from a wild type strain unrelated to the strain which produced *sp* originally, and with no previous history of inbreeding. Reduced fertility seemed to be in effect here, too, for only 29 of the crosses were productive. This frequency, 0.66, corresponds closely to that obtained in the previous crosses involving *sp* and substantiates the observation that this strain is far less fertile than normal strains. The F_1 proved to be entirely normal and an F_2 was produced by two different methods. Part of the F_1 from each cross was allowed to breed with itself. The F_2 in these cases would be inbred for one generation since the parents were siblings. On the other hand, part of each F_1 was bred with the F_1 from another cross. The F_2 produced under these conditions would not be inbred except to the extent that the grandparents were related. While the difference in the degree of inbreeding between these two groups is relatively small, it seemed possible that if the expression of *sp* depended to any great extent upon this factor, it might become apparent by this procedure. However, the results of these experiments indicated that the expression of *sp* was probably not dependent upon the degree of inbreeding, for the inbred F_2 consisted of 962 wild type and 282 mutants, and the crossbred F_2 consisted of 971 wild type and 271 mutants. The proportions of wild type and mutants do not differ significantly between the two groups ($\chi^2 = 0.211$, $P = 0.65$). It is important to note, however, that if the data from the two crosses is combined, the ratio of wild type to mutant departs significantly from the expected 3:1 ratio ($\chi^2 = 10.067$, $P = 0.0016$). Comparing the F_2 ratios from all crosses brings out the fact that in every case there are more wild type and fewer mutants than expected. The shortage of mutants is probably indicative of the degree to which *sp* depresses viability. If the number of wild type is used to calculate the number of mutants expected on the basis of a 3:1 ratio, it appears that only 88 percent of the predicted number of mutants actually survive to the adult stage.

The mutation "Striped"

In the course of examining a culture of the mutant "black" in *Tribolium confusum*, a single female was noted bearing a white stripe running lengthwise along each elytron. This female was isolated and produced offspring consisting of striped and black individuals. The striped beetles, which proved to be females only, were separated to individual vials, and their offspring collected as pupae and sexed in preparation for experiments to determine the inheritance of the mutation. The data presented in Table II indicate that the mutation is a sex-linked semi-dominant with a semi-lethal effect, and it has been designated "Striped" (symbolized *St*). Since all the beetles referred to in Table II are homozygous black, this gene is ignored and black beetles are regarded as wild type. In cross D, where *St* females are crossed with wild type males, if *St* was sex-linked and completely dominant, then the offspring should have consisted of *St* males and females and wild type males and females all in equal proportions.

TABLE I. The F_1 and F_2 from crosses of split with wild type

Parents / Cross	*sp/sp* ♀ × +/+ ♂								*sp/sp* ♂ × +/+ ♀					*sp/sp* ♀ × *sp/sp* ♂		
	A1	A2	A3	A4	A5*	A6	A7	A8	B1	B2	B3	B4	B5	C1	C2	C3
F_1 wild	6	6	9	3	5	26	9	5	0	0	5	45	62	0	0	0
split	0	0	0	0	6	0	0	0	0	0	0	0	0	27	14	5
F_2 wild	33	39	161	0	24	96	13	51	0	0	103	133	108	0	0	0
split	19	8	56	0	18	22	5	17	0	0	33	53	15	29	62	0

F_2 totals of crosses A and B (excluding A5)		test for a 3:1 ratio of wild to split
	wild 737	$\chi^2 = 0.970$
	split 228	$P = 0.33$
	total 965	

*In this cross, the wild male was probably heterozygous for *sp*.

However, the absence of any *St* males and the appearance of three males with entirely white elytra suggested that the expression of the *St* gene alone, in the hemizygous condition, resulted in white elytra, whereas in the heterozygous state the striped phenotype appeared. The recessive lethal effect associated with the *St* gene is indicated by the very low frequency of white males which, in the absence of lethality, should be as frequent as each of the other three classes of individuals. The numbers of individuals in these three classes does not differ significantly from the expected 1:1:1 ratio ($\chi^2 = 4.269$, $P = 0.17$), indicating that the lethal action of *St* is not manifested in the heterozygous state. The beetles from cross D were mated, wild males with wild or *St* females (crosses D1 and D2), and the results confirmed the hypothesis explaining the inheritance and expression of *St*.

Hemizygous white males proved to be quite inviable and crosses involving them were usually unproductive. However, a few of the F_1 white males collected from crosses similar to cross D produced offspring when mated with *St* or wild females. The results of two such crosses, E and G, are given in Table II. The inviability of white females is apparent from their low frequency among the offspring from cross E. White males and females from this group were placed together in vials with the intention of starting a strain of the mutant. However, only one female survived more than a week, and only five offspring were produced, one white female and four white males. Unfortunately, all of these died within a few days. It is now obvious that *St* can be maintained only by using Striped females to start new cultures.

Characterizing *St* beetles is beset by two difficulties. First, the stripes tend to fade and become almost indistinguishable after two weeks. Second, there is a small but troublesome variability in the expression of the mutant gene. Three mutant males have been encountered with a small strip of black running lengthwise along the inner edge of each elytron. These males, which might have been mistaken for Striped individuals, were assumed to be white since they survived only a few days. On another occasion, two phenotypically white females were encountered where only Striped were expected. It seems safe to assume that these isolated instances simply represent variability in the penetrance of *St*, but the possibility of genetic modifiers cannot at present be ruled out.

The viability of *St* homozygous or hemizygous individuals can be estimated from the data of crosses D, D1, E and G1, by comparing the number of white individuals expected with the number actually observed. Under the conditions of these experiments, the lethal action of the *St* gene reduced the viability to about 14.16 percent. Further studies of the pleitropic and dosage effects of the *Striped* mutation and of its behavior in mixed populations are now being contemplated.

Summary

Two newly isolated mutations of *Tribolium confusum* are described. Split proved to be due to a recessive autosomal gene which produces an abnormality of the elytra and lowers viability to about 85 percent of wild type. Striped is a sex-linked semi-dominant with a semi-lethal effect. Heterozygous individuals have elytra bearing white stripes, while in homozygous and hemizygous individuals the elytra are entirely white. The white beetles have a viability of about 15 percent and are quite infertile.

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TABLE II. The phenotypes of the offspring resulting from crosses of Striped and wild type individuals

Parents	Offspring ♀			Offspring ♂		
	+	*St**	*w**	+	*St*	*w*
Cross D						
+/*St* ♀ × + ♂	156	145	0	122	0	3
Cross D1						
+/*St* ♀ × + ♂	52	45	0	70	0	17
Cross D2						
+/+ ♀ × + ♂	96	0	0	98	0	0
Cross E						
+/*St* ♀ × *St* ♂	0	143	26	145	0	13
Cross G						
+/+ ♀ × *St* ♂	0	45	0	43	0	0
Cross G1						
+/*St* ♀ × + ♂	75	67	0	78	0	0

*The symbol *St* indicates the striped phenotype and *w* the white phenotype.

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